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FOREST ECOLOGY AND DISTRIBUTION OF BATS IN ALASKA

A THESIS

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By

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Fairbanks, Alaska

May 1996

FOREST ECOLOGY AND DISTRIBUTION OF BATS IN ALASKA

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Abstract

This thesis documents distribution of bat species in Alaska and effects of clearcutting on bat activity in temperate rainforests of southeastern Alaska. Occurrence of *Myotis lucifugus*, *M. californicus*, *M. volans*, *M. keenii*, and *Lasionycteris noctivagans* is confirmed in southeastern Alaska. I describe new specimens of *M. keenii* from southeastern Alaska, the first in over 100 years. *Myotis lucifugus* and *Eptesicus fuscus* are documented north of 64° N latitude. Environmental conditions and geography which may influence distribution and latitudinal diversity gradients are discussed. Low bat activity in second-growth forests and clearcuts suggests that these areas provide little summer habitat. Higher activity levels in old-growth and riparian forests suggest these areas are important summer habitat. A change in activity between lactation and post-lactation periods is also noted. Unusual aspects of *M. lucifugus* ecology in southeastern Alaska are: consumption of spiders; presence of maternity colonies in a temperate rainforest; and intermittent use of hibernacula.

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Chapter One

Introduction

This study was undertaken to investigate the occurrence and distribution of bat species throughout Alaska, and the effects of timber harvest on bat activity in the temperate rainforests of southeastern Alaska. There has been little documentation of the occurrence of bat species in Alaska, the northwestern range limit of several species. No research in Alaska has previously focused on bat habitats or the effects of habitat modification on bat activity.

The incentive for conducting this study was the lack of information about bat species throughout the state, coupled with intensive habitat modification and forest fragmentation in southeastern Alaska. Investigation of the occurrence, distribution, and habitats of bats in southeastern Alaska is especially timely, because 42% of the most productive forests in southeastern Alaska were clearcut harvested by 1990 (United States Department of Agriculture 1991; 1993) and extensive harvest continues on both public (United States Department of Agriculture *in press*) and private lands.

The aim of this study was to provide scientific data that is useful in managing forest resources on public lands for biological diversity, as mandated by the United States Congress (1970; 1976). The National Environmental Policy Act (United States Congress 1976) requires Federal agencies to consider the environmental consequences of proposed activities that could impact the environment. The National Forest Management Act (United States Congress 1970) states that biological diversity must be considered in the planning process, and inventories must include data that allow an evaluation of potential effects of management plans on biological diversity.

Chapter two investigates distribution and occurrence of bats throughout Alaska. To test whether bat species richness decreases with increasing latitude, I documented

the occurrence of five bat species throughout Alaska, based on verified museum specimens. Environmental factors that may influence the latitudinal gradient of bat species richness in the state are examined. Data in this inventory are the foundation for the following chapters and for future studies on bats throughout Alaska. Chapter three provides information on new specimens of an apparently rare species, *Myotis keenii*, in southeastern Alaska. This chapter investigates the possibility that this species is a regular component of the fauna of southeastern Alaska. Morphological measurements, diet, and habitat information are provided.

Chapter four tests whether timber harvest affects the use of the temperate rainforests in southeastern Alaska by bats. To determine use of these forests by bats, I compared relative bat activity levels in high volume (volume class 5 and 6) old-growth forests, riparian areas, clearcuts, and closed-canopy second-growth forests. In addition, I tested whether activity of bats in old-growth forests and riparian areas differed between July and August or between habitat types by analyzing the nightly pattern of bat activity and relative feeding activity in these habitats. To provide a baseline for future studies on bat ecology in southeastern Alaska, I collected preliminary data on bat diets, *M. lucifugus* reproduction, and seasonal occupation of caves. Chapter five summarizes previous chapters, including the relationship of habitat to southeastern Alaska's bats.

Chapter Two

Latitudinal Limits of Bats in Alaska

Abstract

Bat species in temperate North America are relatively well documented, yet little research has focused on North American bats at the northwestern limit of their ranges. Although only *Myotis lucifugus* occurs throughout most of Alaska, the highest number of bat species is in southeastern Alaska, where the five vespertilionid species comprise 13 percent of the terrestrial mammal species. In this study, field research and investigations of museum holdings documents species occurrence and distribution in Alaska. Six bat species are confirmed from the state: *M. lucifugus, M. keenii, M. californicus, M. volans, Lasionycteris noctivagans*, and *Eptesicus fuscus*. Geographical barriers, roost availability, climate, length of night, and prey abundance that may influence latitudinal gradients and bat distribution are discussed.

Introduction

Alaska encompasses more than 1.5 million km^2 of northwestern North America, an area approximately 15% the size of Canada or 20% the size of the contiguous 48 United States. Across this broad expanse, climatic differences create habitats that vary from coniferous rainforests in the southeastern Alexander Archipelago to boreal forests in central Alaska and treeless tundra on the plains of the Arctic coast (Viereck et al. 1992). The high latitude, large area, and variety of habitats in Alaska provide an opportunity for studying distribution and latitudinal gradients of species at the latitudinal limits of their ranges. There is abundant literature regarding distribution and ecology of bats in North America (Barbour and Davis 1969; Humphrey and Cope 1976; Hall 1981;

van Zyll de Jong 1985; Tuttle 1988; Nagorsen and Brigham 1993). The occurrence of bats in Alaska has been known for over 100 years (Turner 1886), however, there has been no comprehensive documentation of bat distribution in Alaska. Manville and Young (1965) summarized the current knowledge of all bat species in Alaska in a few paragraphs. Their work is weakly supported by literature records and some specimens in the collection of the U. S. National Museum. Hall (1981) places the distribution limit of *M. lucifugus* at Fort Yukon based on sightings of an unidentified bat (Turner 1886).

This chapter investigates bat species occurrence and distributional limits in Alaska. To determine whether bat species richness decreases with increasing latitude, I substantiate distribution and occurrence of bats based on verified museum specimens (Appendix I). I also provide preliminary natural history characteristics that may impact bat distribution, including seasonality and reproductive information. Ecological factors that may constrain or facilitate northward distribution of bat species are considered. Six species of the family Vespertilionidae reach their northern and western limits in Alaska. Species richness of bats in Alaska is highest in the southeastern panhandle where five species constitute 13% of the species of terrestrial mammals: *Myotis lucifugus* (little brown bat), *M. californicus* (California bat), *M. volans* (long-legged bat), *M. keenii* (Keen's bat), and *Lasionycteris noctivagans* (silver-haired bat). Only *M. lucifugus* occurs widely in the state. *Eptesicus fuscus* (big brown bat) is known from one specimen from central Alaska. Previously, most bat species were documented by a few specimens collected by early naturalists (Heller 1909; 1910; Swarth 1911; Grinnell 1918; Miller and Allen 1928) and records for Alaska represented incidental captures rather than a systematic search for bats. New records, based on efforts in this study, have bolstered the documentation of bats in Alaska. A systematic inventory of bats in the state remains to be completed.

Methods

The distribution and occurrence of bat species in Alaska were investigated through field studies and analysis of museum collections. Field studies were conducted primarily from 1990 to 1995 in southeastern Alaska (Chapter 3; West 1993; MacDonald and Cook 1994; Parker and Cook *in press*; Parker et al. *in press*). A total of 195 bat specimens from throughout Alaska are archived at the University of Alaska Museum from these field studies and from previous collectors. In addition, 25 major North American museums were contacted for information about their Chiroptera holdings from Alaska (Appendix II). Thirteen of these museums had a total of 101 bat specimens from Alaska. All specimens were examined and identifications were confirmed. Taxonomy follows Koopman (1993), and I used external and cranial characteristics to identify species (van Zyll de Jong 1985). Records of bat sightings were considered marginally useful because of the similar appearance of North American vespertilionids in flight.

To determine whether female bats raise their young in Alaska, locations of maternity colonies (aggregations of female bats with their young) were noted. To compare the male:female ratio of *M. lucifugus* in summer with the summer sex ratio noted in coastal Oregon, the number of male and female *M. lucifugus* captured in southeastern Alaska between June and August 1991-1994 were counted. This was the only group for which adequate data were available. The sex ratio was tested using χ^2 tests of independence ($P \leq 0.05$). Female reproductive status was also noted.

Results

Bat occurrence and distribution in Alaska has been substantiated by specimens housed in 14 museums (Appendix I). Distributions are detailed in the following species accounts.

Myotis lucifugus (Le Conte 1831)

Myotis lucifugus (little brown bat) is the most common and widely distributed bat in Alaska. North American museums contain 279 specimens of *M. lucifugus* which were collected in 54 locations in Alaska (Appendix I; Figure 1; Figure 2). This species composes 94% of all bat specimens from the state, and 92% of the bat specimens from southeastern Alaska. Because collection effort has been sporadic, these specimens may not necessarily reflect the regional abundance or range limits of this species. Nonetheless, these specimens do document known range limits, season of occurrence, and the abundance of this species relative to other bat species in Alaska. The northern and western-most specimens of *M. lucifugus* are from Minto (65° 00' N, 148° 49' W) and Sleetmute (61° 42' N, 157° 10' W), respectively. The southern-most specimen is from Essowah Lakes (54° 47' N, 132° 52' W) on Dall Island in the southwestern part of the Alexander Archipelago. Most specimens from Alaska were collected between 1 June and 31 August. Exceptions are: one female *M. lucifugus* collected at College (64° 50' N, 147° 50' W) on 26 May 1948 (UMDZ collection); four females and one male *M. lucifugus* collected on Kodiak Island (57° 20' N, 153° 22' W) on 12 February 1883 (USNM collection); three females and one male *M. lucifugus* collected at Loring (55° 36' N, 131° 39' W) 17-22 September 1895 (USNM collection); and one male and one unsexed *M. lucifugus* collected at Ketchikan (55° 20' N, 131° 38' W) during October 1909 (USNM collection).

Of the 36 female and 41 male *M. lucifugus* collected in southeastern Alaska between June and August 1991 through 1994, the female:male ratio was not significantly different from 50:50 (χ^2, $P \leq 0.05$). Reproductive status was available for 15 of these females. Two pregnant females were collected on 13 June 1993; nine lactating individuals were collected between 15 June and 7 August; and four females, which were not pregnant or lactating, were collected between 28 June and 19 August. On 11 August 1993, a juvenile male *M. lucifugus* was collected at Red Creek on Prince

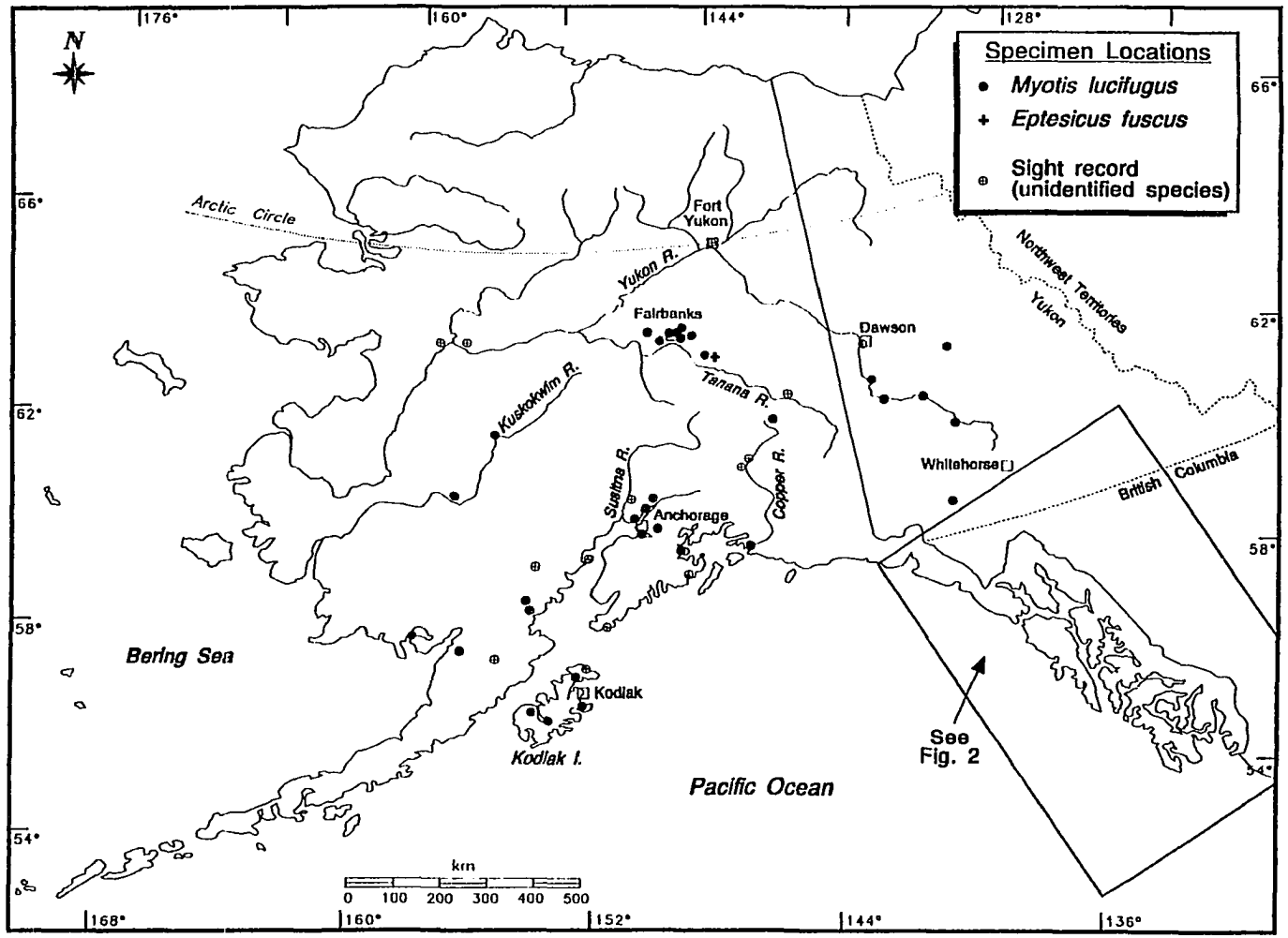


Figure 1. Location of bat specimens collected in Alaska.

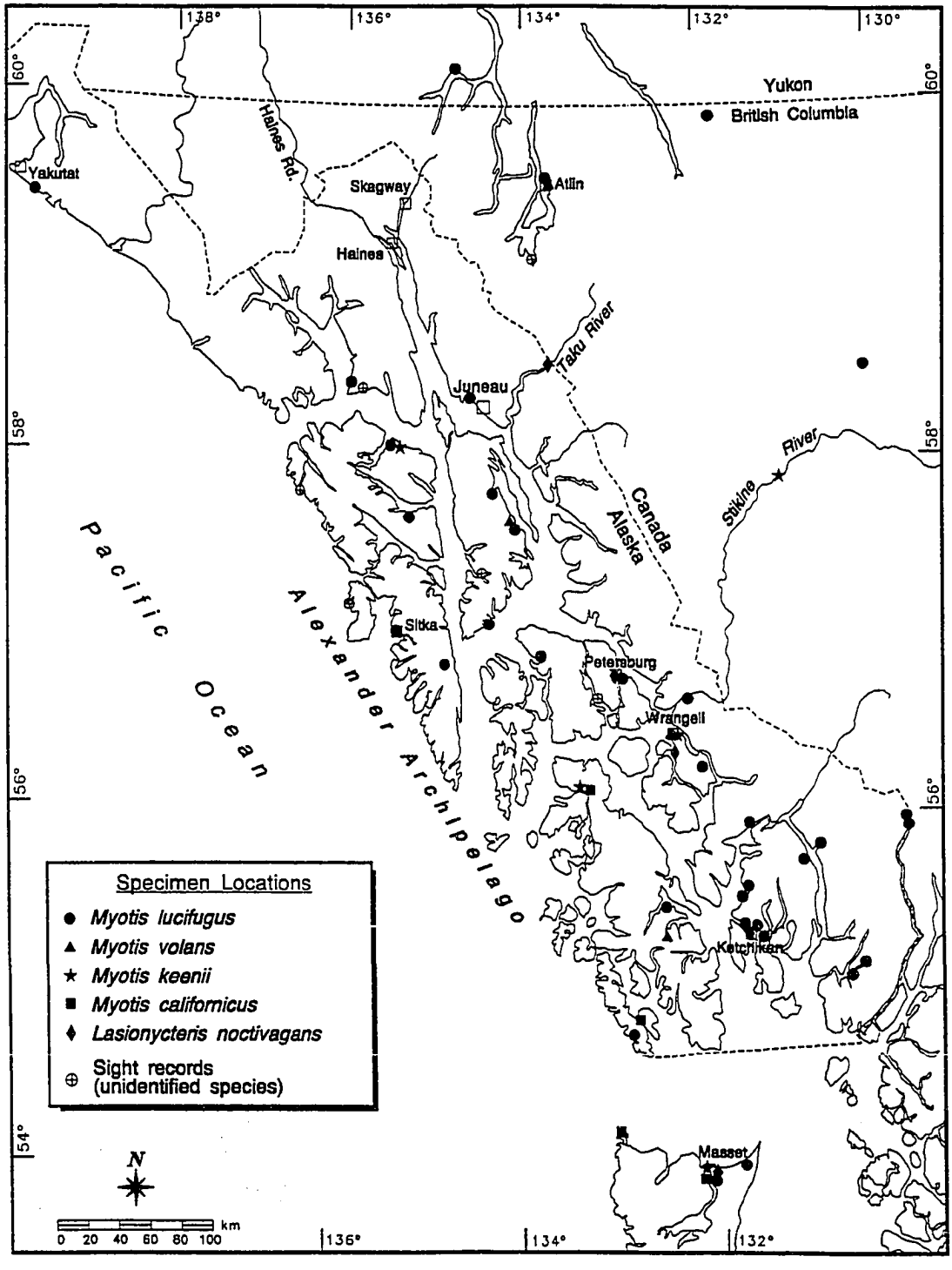


Figure 2. Location of bat specimens collected in southeastern Alaska and selected localities in neighboring Canada.

of Wales Island (56° 15' N 133° 8' W; UAM 24816). This suggests that young bats in southeastern Alaska fledge by mid-August. In addition, 34 female *M. lucifugus* were collected from a maternity colony in a house attic at Hyder (55° 55' N, 130° 1' W) on 10 June 1990. Twenty-eight were pregnant, five were not pregnant or lactating, and reproductive data was not available for the remaining individual. Hyder is located on the mainland, near the Canadian border at the head of Portland canal, and could be influenced by the continental climate of British Columbia. Maternity colonies of *M. lucifugus* also have been located in man-made structures at Salcha (64° 28' N, 146° 53' W; Whitaker and Lawhead 1992), near Mentasta Lake (62° 54' N, 143° 45' W; Parker unpublished data), between Wasilla and Anchorage (61° N, 149° W; J. Hughes *personal communication*, 1990), in the Glacier Bay Lodge at Bartlett Cove (58° 27' N, 135° 53' W; UAM collection), at Hoonah, (58° 06' N, 135° 26' W; UAM collection), Loring (55° 36' N, 131° 39' W; UAM collection), Hyder (55° 55' N, 130° 1' W; UAM collection), and Ketchikan (55° 20' N, 131° 38' W; Parker unpublished data).

In addition to *M. lucifugus* specimens (Appendix I), numerous sightings of unidentified bats have been reported from a variety of locations in Alaska. The two northern-most records of *M. lucifugus* depicted by Hall (1981) are Fort Yukon (66° 34' N, 145° 16 W) and Nulato (64° 43' N, 158° 06' W). These records were traced to Turner (1886), who reported that an "unidentified species of bat was reputed to inhabit these locations in summer." Bats are routinely observed along the Yukon river (66° N, 146° W) in the summer (B. E. Lawhead *personal communication*, 1993). While it is reasonable to assume that bats sighted in central Alaska are *M. lucifugus*, in southeastern Alaska the occurrence of other species makes such assumptions unreliable.

The range of *M. lucifugus* extends across Canada, through most of the United States, and south into the central highlands of Mexico (Hall 1981; van Zyll de Jong 1985). This species occurs throughout the southern half of the adjacent Yukon Territory Canada, with at least 61 specimens collected in 11 locations. Sightings

assumed to be *M. lucifugus* have been recorded in at least three other locations in the Yukon Territory, the northern-most at Dawson (64° 4' N, 139° 20' W; Youngman 1975). This species has also been recorded at Hay River (60° 52' N, 115° 44' W) in the Northwest Territories and throughout British Columbia (van Zyll de Jong 1985).

***Myotis volans* (H. Allen, 1866)**

Five specimens of *Myotis volans* (long-legged bat) are recorded for Alaska, all from the Alexander Archipelago (Appendix I; Figure 2). The first specimen (MVZ 186) was collected on 9 June 1907 at Mole Harbor, Admiralty Island (57° 40' N, 134° 3' W) during the Alexander Alaska Expedition (Heller 1909). The specimen was originally mis-identified as *M. lucifugus alascensis*. Grinnell (1918) did a comparative study of the bats of Alaska and British Columbia in which she corrected the identity of this specimen. On 29 July 1991, three unsexed *M. volans* were collected in Wrangell (56° 28' N, 132° 22' W; West 1993). The fifth specimen of *M. volans* (UAM 24822) was a female collected on 19 July 1993 at Polk Inlet on Prince of Wales Island (55° 20' N 132° 30' W). *Myotis volans* has been collected widely in British Columbia. The location nearest Alaska, and the most northern record of this species is Atlin (59° 34' N, 133° 42' W; Cowan and Guiguet 1960; van Zyll de Jong 1985). This species occurs from Alaska, British Columbia, and Alberta through western North America to central Mexico (Hall 1981; van Zyll de Jong 1985).

***Myotis keenii* (Merriam, 1895)**

The occurrence of *Myotis keenii* (Keen's long-eared bat) in Alaska has been substantiated by three specimens (Appendix I; Figure 2; Parker and Cook *in press*). The first, (USNM 187394, unsexed; Miller and Allen 1928), was collected on 9 June 1887 at Fort Wrangell (now known as Wrangell) on Wrangell Island in southeastern Alaska (56° 28' N, 132° 22' W). Like the first specimen of *M. volans*, it was initially mis-identified

as *M. lucifugus alascensis* (Miller 1897), and corrected by Grinnell (1918). The second specimen of *M. keenii* (UAM 23338, male) was captured on 20 July 1993 at Turn Creek on northern Prince of Wales Island (56° 10' N, 133° 18' W), approximately 65 km SW of Wrangell (Figure 2; Parker and Cook *in press*). This bat was captured in a mist net at 23:20 (two h 10 min after sunset) as it flew within 1 m of a limestone cliff and 1 m above the water. The third specimen (UAM 29831, male) was collected on 11 July 1994 from a maternity roost of *M. lucifugus* in the attic of an operating fish cannery at Hoonah on Chichagof Island (58° 06' N, 135° 26' W), approximately 160 km N of the Wrangell specimen (Figure 2; Parker and Cook *in press*).

Myotis keenii was previously thought to be conspecific with the northern long-eared bat, *M. septentrionalis*, but is now considered a separate species (van Zyll de Jong 1979). These two species also are difficult to distinguish from the western long-eared bat, *M. evotis*, which is sympatric with *M. keenii* in British Columbia and Washington. The three species are differentiated by discriminant function analysis of cranial measurements (van Zyll de Jong 1979; van Zyll de Jong and Nagorsen 1994). The few locality records suggest that the range of *M. keenii* is restricted to Pacific coastal forests from western Washington to southeastern Alaska (Nagorsen and Brigham 1993; van Zyll de Jong and Nagorsen 1994). The type locality for *M. keenii* is Massett, on Graham Island (54° 01' N, 132° 06' W) in the Queen Charlotte Islands of British Columbia. This species has been collected as far north as Telegraph Creek (57° 54' N, 131° 10' W) in British Columbia (USNM 209856; van Zyll de Jong 1985).

***Myotis californicus* (Audubon and Bachman, 1842)**

The first four specimens of *Myotis californicus* (California bat) in Alaska were collected as mummies or skeletons from caves on Long (54° 52' N, 132° 48' W; Grinnell 1918) and Prince of Wales (56° 10' N, 133° 19' W) islands of the Alexander Archipelago (Appendix I; Figure 2). The only live *M. californicus* recorded (UAM

20498, female) was collected during February 1992 in El Capitan Cave on Prince of Wales Island (56° 10' N, 133° 19' W). These five records for *M. californicus* represent the northern range limit of this species, which extends through western North America to southern Mexico (Hall 1981; van Zyll de Jong 1985). The nearest specimens in British Columbia are from the Queen Charlotte Islands at Massett (54° 01' N, 132° 06' W; van Zyll de Jong 1985), the type locality for *M. californicus caurinus* (Hall 1981).

***Lasionycteris noctivagans* (Le Conte, 1831)**

Four female *Lasionycteris noctivagans* (silver-haired bat) have been collected from southeastern Alaska during winter (Figure 2). The first specimen (AMNH 213141, juvenile) likely was hibernating in a boat shed on the Taku River near Juneau (58° 43' N, 133° 40' W) in November 1964 (Barbour and Davis 1969). The second *L. noctivagans* (UAM 20768) was found dead in a wood pile at Wrangell (56° 22' N, 132° 22' W) during February 1992. The third specimen (UAM 30100) was found dead clinging to the side of a house in Petersburg (56° 45' N, 132° 56' W) on 1 January 1995, and the fourth (UAM 30099) was found alive in a house entryway in Ketchikan (55° 20' N, 131° 38' W) on 5 January 1995. These last two specimens were collected when the day-time temperature was about -7° C.

Lasionycteris noctivagans is a migratory, tree-dwelling species (Barbour and Davis 1969; van Zyll de Jong 1985) that occurs throughout southern Canada and most of the United States (Hall 1981; van Zyll de Jong 1985). Although *L. noctivagans* has been reported as far north as Prince William Sound in Alaska (Manville and Young 1965), no specimens were located to substantiate this claim. *Lasionycteris noctivagans* has been collected in British Columbia at Massett (54° 01' N, 132° 06' W) and Skidegate (53° 15' N, 132° 01' W) on the Queen Charlotte Islands, and as far north as the Peace River and Spatsizi Plateau (57° N, 127° W) on the mainland (Schowalter et al. 1978; van Zyll de Jong 1985; Nagorsen and Brigham 1993).

***Eptesicus fuscus* (Palisot de Beauvois, 1796)**

Eptesicus fuscus (big brown bat) has been collected once in Alaska: in the interior of the state, north of the Alaska Range (Appendix I; Figure 1). William D. Berry collected an adult female (UMDZ 111095) from a cabin by the mouth of Shaw Creek, near Big Delta (64° 29' N, 145° 5' W) on 5 September 1955 (Reeder 1965). The nearest record of this species in Canada is at Pine Lake in northern Alberta (52° N, 113° W). The range of *E. fuscus* extends from southern Canada throughout North America to the Caribbean Islands and northern South America (Hall 1981; van Zyll de Jong 1985). Because the location of the Alaska specimen is approximately the same distance outside the range of *E. fuscus* as it is outside the range of *E. nilssonni*, in Siberia, the Shaw Creek specimen was compared with an *E. nilssonni* key (Ognev 1962). The characteristics of the Alaska specimen are those described by van Zyll de Jong (1985) for *E. fuscus* and overall dimensions are larger than those described by Ognev (1962) for *E. nilssonni*. Therefore, the Alaska specimen was considered to be *E. fuscus*. Reports by Manville and Young (1965) and Barbour and Davis (1969) that *E. fuscus* occurs in southeastern Alaska were not verifiable.

Discussion

Bats exhibit a latitudinal gradient worldwide, with higher species richness at lower latitudes (Findley 1993). While latitudinal gradient often is used to explain decreased number of species toward the poles, no single formula explains the mechanism driving this gradient (Huston 1994). In Alaska, *M. lucifugus* occurs throughout most forested regions, at least as far as 65° N latitude, whereas the other four species appear to reach their northern limits south of 59° N latitude in the temperate rainforests of southeastern Alaska. None of the species appear to be abundant. Furthermore, it is unclear whether all five species occur throughout

southeastern Alaska, or whether some, such as *M. californicus*, reach their northern limits south of 57° N. The following discussion considers current knowledge of bat distribution in Alaska and factors which may influence latitudinal gradients of bats across Alaska.

Species Distribution and Seasonality

The known range limits of bat species in Alaska have been clarified by compiling records of known specimens and noting previously published specimen locations that are based only on sight records. These investigations support evidence by early naturalists (Heller 1909; Swarth 1911; Grinnell 1918; Miller and Allen 1928) that *M. lucifugus*, *M. keenii*, *M. californicus*, and *M. volans* are a regular part of the southeastern Alaska fauna. This study has also confirmed that *L. noctivagans* is present in southeastern Alaska (Barbour and Davis 1969), but raise doubts that this species occurs in southcentral Alaska, or that *E. fuscus* normally occurs in the state (Manville and Young 1965; Barbour and Davis 1969). Investigations indicate that only *M. lucifugus* occurs throughout most of Alaska. Bats have been documented only from forested regions of the state, and do not appear to extend their ranges to the treeless regions such as the Arctic coast tundra and windswept Aleutian Islands.

According to Rapoport's rule, there is a positive correlation between the latitude at which species occur and the latitudinal extent of their ranges. Species at higher latitudes have larger geographical ranges because wide temperature ranges and extreme cold at high latitudes favor species with wide climatic tolerance. Therefore, individuals of these northern species are less restricted in their habitat use (Stevens 1989). One such species is *M. lucifugus*, which occurs farther north than other bat species in North America. *Myotis lucifugus* is documented from Alaska's boreal forests in summer. Bat sightings at Fort Yukon, and along the Yukon river suggests that this species occurs in forested areas north of the Arctic Circle. *Myotis lucifugus* also occurs in southeastern Alaska rainforests and its range extends south to the warm, arid regions of North and

Central America (Hall 1981). Tolerance of a wide range of habitats is also reflected in the variety of prey consumed (Chapter 4; Buchler 1976; Anthony and Kunz 1977) and variety of roosts occupied by *M. lucifugus* (Barclay and Cash 1985; Nagorsen and Brigham 1993; Bradshaw *in press*; Vonhof *in press*).

Myotis lucifugus occurs in the southern parts of Alaska year-round. This species has been observed hibernating in southeastern Alaska in winter (personal observation), and was collected on Kodiak Island in February. Whether *M. lucifugus* migrates from northern latitudes of central Alaska to hibernate in milder southern regions along the coast is unknown. Bats commonly are observed in Fairbanks (64° 50' N, 147° 30' W) in early October. On 7 May 1994, bats were observed foraging over a pond near the Tanana River (64° 40' N, 148° 15' W), just after river ice break-up (C. T. Seaton *personal communication* 1994). These observations suggest that *M. lucifugus* either quickly migrate long distances to milder climates or hibernate in the vicinity of these sightings. For bats which summer near Fairbanks, migrating south to hibernate would likely require traveling more than 400 km across the Alaska Range to milder coastal regions. *Myotis lucifugus* in Ontario Canada travel at least 220 km to hibernate (Fenton 1970). In contrast to such studies of *M. lucifugus* in North America (Humphrey and Cope 1976), *M. dasyeneme, M. daubentoni, M. mystacinus, M. nattereri, Plecotus auritus,* and *Eptesicus nilsonni* summer in the central and northern parts of European Russia and also hibernate in the caves of that region (Strelkov 1969). Further investigation could clarify whether *M. lucifugus* hibernate in central Alaska where they spend the summer, or migrate to milder regions such as southcentral and southeastern Alaska.

The small number of *M. keenii*, *M. californicus*, and *M. volans* specimens collected do not provide enough data to infer whether these species inhabit southeastern Alaska year-round. I suggest however, that they are year-round residents. *Myotis keenii* inhabits coastal old-growth forests in Alaska, British Columbia, and Washington (van Zyll de Jong 1985; van Zyll de Jong and Nagorsen 1994; Parker and Cook *in*

press). Because this apparently rare species has not been documented outside Pacific coastal forests, it is presumed to be nonmigratory and therefore, a permanent resident of southeastern Alaska. The five specimens of *M. californicus* from the southern tip of southeastern Alaska represent the northern-most locality records for this species (Appendix I; Hall 1981). *Myotis californicus* is thought to be nonmigratory (Barbour and Davis 1969). Therefore, this bat likely occurs in southeastern Alaska year-round. *Myotis volans* is also considered nonmigratory (Barbour and Davis 1969), so is probably also a permanent resident of southeastern Alaska.

The known distribution of *L. noctivagans* in Alaska is limited to the southeastern panhandle (Figure 2). The recent specimens collected in southeastern Alaska confirm that *L. noctivagans* occurs in those coastal rainforests (Barbour and Davis 1969; Hall 1981). Further investigation into the seasonality of *L. noctivagans* would be helpful in determining whether females migrate to southeastern Alaska in winter, as the four documented specimens suggest, or whether both sexes of this species occur in those northern rainforests throughout the year, as appears to be the case in Pacific coast forests of southwestern British Columbia (Schowalter et al. 1979).

A specimen on which Manville and Young (1965) based their claim that *E. fuscus* occurs in southeastern Alaska near Juneau could not be located. The only specimen located was the adult female collected in central Alaska at Shaw Creek near the Richardson Highway (UMDZ 11095; Reeder 1965). Because the Shaw Creek specimen was more than 1600 km outside the known range of *E. fuscus*, this specimen was most likely an accidental visitor, as Reeder (1965) suggested.

Environmental Factors

Climate is likely to be the most important environmental factor determining bat distribution in Alaska. The warm Japanese ocean current moderates the climate in southeastern Alaska, and the difference between mean January low and mean July high temperature is 25°C compared with 51°C in central Alaska near Fairbanks. Extremely

low winter temperatures and areas of permafrost could limit the number of bat hibernacula in central Alaska. The cold, dry climate of more northern Alaska regions may hinder distribution of all bat species, since nonfreezing, humid sites suitable for hibernation are likely to be limited.

In addition to temperature, precipitation is likely to affect bat species distribution. Annual precipitation in southeastern Alaska ranges from 1,000 to 8,100 mm and heavy rains occur in all seasons (Hartman and Johnson 1984). In similar temperate rainforests on the western slopes of the Cascade mountains of Oregon, Thomas (1988) found that the sex ratio of *M. lucifugus* was skewed toward male bats and no reproductive females occurred. He concluded that this was probably due to extended periods of rain which limited foraging time and caused bats to go into torpor to conserve energy. Torpor slows fetal growth and milk production (Racey 1973). Moreover, pregnant and lactating females do not fully utilize the energy-savings of torpor, even when food is not available (Kurta 1990). These conditions may make it energetically advantageous for female *M. lucifugus* to avoid rainy climates. Precipitation also decreased reproductive success of this species during rainy years in more arid regions of British Columbia (Grindal et al. 1992). In southeastern Alaska, however, the distribution of female *M. lucifugus* is not limited by high precipitation. The equal sex ratio of *M. lucifugus* in southeastern Alaska suggests that females tolerate the wet climate. Although the ratio of reproductive to nonreproductive females is not known, the occurrence of maternity colonies suggests that other factors allow *M. lucifugus* females to raise their young in this cool, rainy climate.

Climatic conditions that cause the rainforest environment of southeastern Alaska also moderate temperature extremes, creating a mild climate. This could be a factor which enables *M. lucifugus* as well as *M. volans*, *M. californicus*, *M. keenii*, and *L. noctivagans* to extend their ranges north and west into southeastern Alaska. Cool summer temperatures and the high rainfall of southeastern Alaska, however, probably restrict westward expansion of the big brown bat into southeastern Alaska. This species

occurs in the dry climate of the neighboring interior of British Columbia at the same latitude (Nagorsen and Brigham 1993).

The geography of southeastern Alaska possibly also limits bat distribution. Southeastern Alaska is isolated geographically and climatologically from British Columbia and southcentral Alaska by a chain of high mountain peaks and extensive ice fields along the mainland coast. These mountains are a barrier for other mammals, although major rivers provide corridors for dispersal (Klein 1965; Lance 1995). The length of the Alexander Archipelago, from 54° N to 59° N latitude (555 km) and its many, various sized islands may also limit bat species distribution. On Scandinavian islands, bat species richness declines with increased distance from the mainland, increased latitude, and decreased island size (Ahlen 1983). Further studies of bat species richness and distribution in the Alexander Archipelago are necessary to confirm such latitudinal and island biogeographical gradients in southeastern Alaska.

Availability of roosts limits bat distribution and abundance in temperate climates (Humphrey 1975; Kunz 1982*a*). *Myotis lucifugus*, *M. volans*, *M. californicus*, *M. keenii*, and *L. noctivagans* roost under loose bark or in snags and hollow trees (Kunz 1982*b*; Barclay and Cash 1985; Christy and West 1993; Bradshaw *in press*; Vonhof *in press*). The temperate rainforests of southeastern Alaska contain abundant live trees, snags, and fallen logs in a variety of sizes (Alaback 1991). Such structural diversity provides hollows suitable for cavity-roosting species (Bunnell and Allaye-Chan 1984) such as bats (Barclay and Cash 1985; Christy and West 1993; Bradshaw *in press*; Vonhof *in press*). Extensive karst formations in the Alexander Archipelago (Buddington and Chapin 1929; Baichtal 1993) provide numerous caves and crevices, where hibernating bats have been observed and collected (UAM collection). Hot springs are also abundant throughout the Alexander Archipelago (Waring 1917; Motyka and Moorman 1983). *Myotis lucifugus* roost among heated boulders at White Sulfur Springs on Chichagof Island, and unknown species of bats roost in geothermally heated bath houses on Bell Island (Parker, unpublished data). The increased warmth of these

roosts gives thermal advantages similar to house attics, and the importance of these sites as maternity roosts should be investigated. The abundance of these different types of roosts suggests that hibernacula and summer roosting sites are not a limiting factor in southeastern Alaska.

Although roost sites are abundant in the Alexander Archipelago of southeastern Alaska, lack of hibernacula and summer roost sites are likely to limit bat distribution elsewhere in the state. In the remainder of Alaska, forests are less dense, and trees are smaller, suggesting limited roost availability. The long, cold and dry winters in central Alaska make nonfreezing, humid hibernacula especially important. No hibernacula have been recorded in central, southwestern, or southcentral Alaska, although a *M. lucifugus* skeleton collected from a Chitistone River cave (UAM 30213) suggests that this species attempts to hibernate as far north as 61° 26' N. This cave is relatively humid and apparently does not freeze in winter (S. W. Lewis *personal communication 1995*). Limestone formations also occur in the Lime Hills (61° 50' N, 154° 20' W; Gilbert et al. 1990) and White Mountains (62° 00' N, 155° 00' W; Blodgett and Gilbert 1983) and may contain humid caves that do not freeze and are suitable for hibernation. These sites have not been investigated due to their remoteness. Other possible hibernacula include well-insulated buildings. No aggregations of hibernating bats have been located in Alaska, other than in the southeastern part of the state and possibly on Kodiak Island. A concentrated winter survey of caves and house attics that remain above freezing would help determine whether *M. lucifugus* which summer in central, southwestern, and southcentral Alaska also hibernate in those regions.

Bat populations in Alaska also may be affected by prey availability. Insect abundance often is decreased by cool or rainy weather (Johnson 1969). Prey abundance and nightly insect activity patterns have not been investigated in Alaska, and prey abundance could be high, despite cool or rainy conditions. Prey analyses for *M. lucifugus* indicate that spiders constitute 15% of their diet in southeastern Alaska (Chapter 4) and 16% in central Alaska (Whitaker and Lawhead 1992). In southeastern

Alaska spiders also constituted 5% of the stomach contents of a single *M. volans*, and 40% of the stomach contents of a single *M. keenii* specimen (Chapter 4). Although spiders are common prey of *M. volans* (Whitaker et al. 1977; Whitaker et al. 1981) and the diet of *M. keenii* has not been reported elsewhere for comparison, this high percentage of nonflying prey is unusual for *M. lucifugus* (Chapter 4). This species, however, is known to feed on a wide variety of prey (Buchler 1976; Fenton and Morris 1976). I suggest that the high percentage of spiders in the diet of Alaska *M. lucifugus* reflects the ability of this species to adapt to habitats ranging from the central highlands of Mexico to Alaska's temperate rainforests and sub-arctic boreal forests.

Because bats are nocturnal, the decreasing length of darkness in summer months at high latitudes could limit their distribution in Alaska. Short nights, which limit foraging time could prevent bats from acquiring enough energy (Anthony and Kunz 1977) or calcium (Barclay 1994) to meet the needs of pregnancy and lactation. Risk of predation by diurnal raptors is likely the greatest constraint limiting day-time foraging by bats (Rydell and Speakman 1995) such as *M. lucifugus* in southcentral, southwestern, and central Alaska. In central Alaska, *M. lucifugus* have been observed foraging among overhanging willows along sloughs and rivers in late evening before sunset (B. E. Lawhead *personal communication* 1994; G. H. Jarrell *personal communication* 1995). These bats apparently avoid risk of day-time predators, such as falcons and hawks (Baker 1962; Byre 1990; Rydell and Speakman 1995) by foraging among shadowy vegetation. *Eptesicus nilssoni* in Sweden (65° N) have also been observed beginning and ending their foraging in daylight (Rydell 1989). In southeastern Alaska, bats do not forage until after sunset and complete most foraging activity 3 h before sunrise (Parker et al. *in press*). This suggests that night length does not limit foraging time in southeastern Alaska.

Conclusion

The range and distribution limits of the five bat species in Alaska have been refined in this study. Furthermore, investigations suggest that *E. fuscus* is not a regular member of Alaska's fauna. *Myotis lucifugus* is the widest ranging species, occupying habitats with a broad range of environmental conditions: from temperate rainforests of the southeastern Alaska Alexander Archipelago to central Alaska's dry continental climate and short summer nights. The wide geographic range of *M. lucifugus* and its apparent ability to utilize a variety of prey may enable this species to tolerate extreme temperature variation and short nights at the northern parts of its range in Alaska, as well as the mild, but wet climate of southeastern Alaska. *Myotis keenii*, *M. californicus*, *M. volans*, and *L. noctivagans* appear to occur only in southeastern Alaska, south of 59° N latitude. All five bat species likely occur in southeastern Alaska year-round, with the possible exception of *L. noctivagans*. Because of the relatively mild winters in southeastern Alaska compared to interior British Columbia it is likely that *L. noctivagans* migrates to southeastern Alaska in winter. *Myotis lucifugus* likely migrate from northern regions to milder, more southern parts of Alaska. Nonetheless, limestone areas in central Alaska may contain suitable winter hibernacula. Further investigation would clarify patterns of distribution, abundance, and reproduction of all bat species throughout Alaska.

Bats in Alaska exhibit a latitudinal gradient, with more species at the lower latitudes in the states. Further investigation of climatic tolerance, hibernation, roost selection, prey abundance, nutritional constraints, and foraging habits at range limits will help determine the factors influencing latitudinal constraints. Analysis of genetic relationships among populations may shed light on whether bat populations in Alaska are isolated from other, nearby populations.

Chapter Three

The Keen's Long-eared Bat, (*Myotis keenii*, Vespertilionidae) in Southeastern Alaska

Abstract

The distribution of *Myotis keenii* is apparently restricted to the Pacific coastal forests of northwestern North America. Although a specimen of *M. keenii* was collected in Alaska in 1887, uncertainty about whether this species is a resident of southeastern Alaska has persisted. Two new records of *M. keenii* from southeastern Alaska are described. Measurements, diet, and habitat information on this poorly documented member of the Pacific Northwest's mammalian fauna are provided.

Introduction

Of the five vespertilionid species occurring in southeastern Alaska, the Keen's long-eared bat (*Myotis keenii*) was last reported in 1887 when an unsexed specimen was taken at Wrangell (USNM 187394; Miller and Allen 1928). This specimen is preserved in alcohol and the skull is not available to confirm its identification. There has been uncertainty about whether this specimen was mis-identified or an accidental record. Because *M. keenii* is distributed throughout coastal rainforests, extensive timber harvest in these forests has increased the need for documenting the status of this species in southeastern Alaska. This chapter provides information on two new specimens of this apparently rare species, in southeastern Alaska. I also investigate the possibility that *M. keenii* is a regular component of the fauna of southeastern Alaska. Morphological measurements, diet, and habitat information are provided.

Myotis keenii was previously regarded as conspecific with the northern long-eared bat (*M. septentrionalis*), but is now considered to be a separate species (van Zyll de Jong 1979). These species are difficult to distinguish from each other, and from the western long-eared bat (*M. evotis*), which is sympatric with *M. keenii* in British Columbia and Washington. The three species can be identified by discriminant function analysis of cranial and external measurements (van Zyll de Jong 1979; van Zyll de Jong and Nagorsen 1994).

Previous to the capture of the specimens described in this paper, only 59 specimens of *M. keenii* have been collected and deposited in museum collections. Thirty-five are from the Queen Charlotte Islands of British Columbia, 9 from other regions of British Columbia, 14 from Washington, and 1 from Wrangell Alaska (van Zyll de Jong and Nagorsen 1994). This suggest that the range of *M. keenii* is restricted to Pacific coast rainforests (Nagorsen and Brigham 1993; van Zyll de Jong and Nagorsen 1994), and extends over 2,000 km from southwestern Washington to southeastern Alaska (Figure 3). Habitat requirements of *M. keenii* are poorly understood (Nagorsen and Brigham 1993), but it apparently roosts in snags, hollow trees, rock crevices and caves (van Zyll de Jong 1985). The apparent rarity of this species and lack of ecological data have prompted the British Columbia Ministry of Environment to place *M. keenii* on the provincial "red list" of species under consideration for listing as threatened or endangered (Nagorsen and Brigham 1993). The species has no special conservation status in the United States.

Methods

During 18 nights in June, July, and August 1993, mist nets were placed in riparian areas on Prince of Wales and Revillagigedo islands. Nets were dismantled either when bat activity was less than two bat passes per hour, or at dawn. Activity was determined with a countdown mode ultrasonic bat detector (Anabat II, Titley Electronics, Ballina N. S. W. Australia). In 1994, bats were collected from a maternity

roost of *Myotis lucifugus* in a fish cannery at Hoonah on Chichagof Island (58° 06' N, 135° 26' W; Figure 3). Captured bats were prepared as voucher specimens (Handley 1988; UAM collection). Specimens and frozen tissue samples are archived at the University of Alaska Museum. Stomach contents collected in 1993 were preserved in 70% ethanol and analyzed for prey volume using standard procedures (Kunz and Whitaker 1983). Species identity was determined using discriminant function analysis of cranial and external measurements (van Zyll de Jong 1979; van Zyll de Jong and Nagorsen 1994).

To provide habitat associations, habitat types were delineated within a 0.8 km radius area surrounding the Turn Creek capture site. Habitat types were determined using soil, landform, (United States Department of Agriculture 1994), and vegetation data (DeMeo et al. 1992). Units were further separated if an area had evidence of disturbance, such as timber harvest, road building, or rock excavation. While foraging distance for *M. keenii* is not known, Anthony et al. (1981) have shown *M. lucifugus* to forage up to 3 km from day roosts. Habitat types within a smaller area surrounding the capture site were delineated because this was a more conservative area.

Results

On 20 July 1993 an adult male *M. keenii* (UAM 23338) was collected at Turn Creek, in a karst region of northern Prince of Wales Island (56° 10' N, 133° 18' W), approximately 65 km SW of Wrangell (Figure 3). This bat was captured in a mist net at 23:20 (2 h 10 min after sunset) within 1 m of a limestone cliff and 1 m above the water. No other bats were captured that night, although other *Myotis* were detected nearby with ultrasonic bat detectors. The four *Myotis* species that occur in southeastern Alaska could not be unequivocally distinguished by their echolocation calls. The

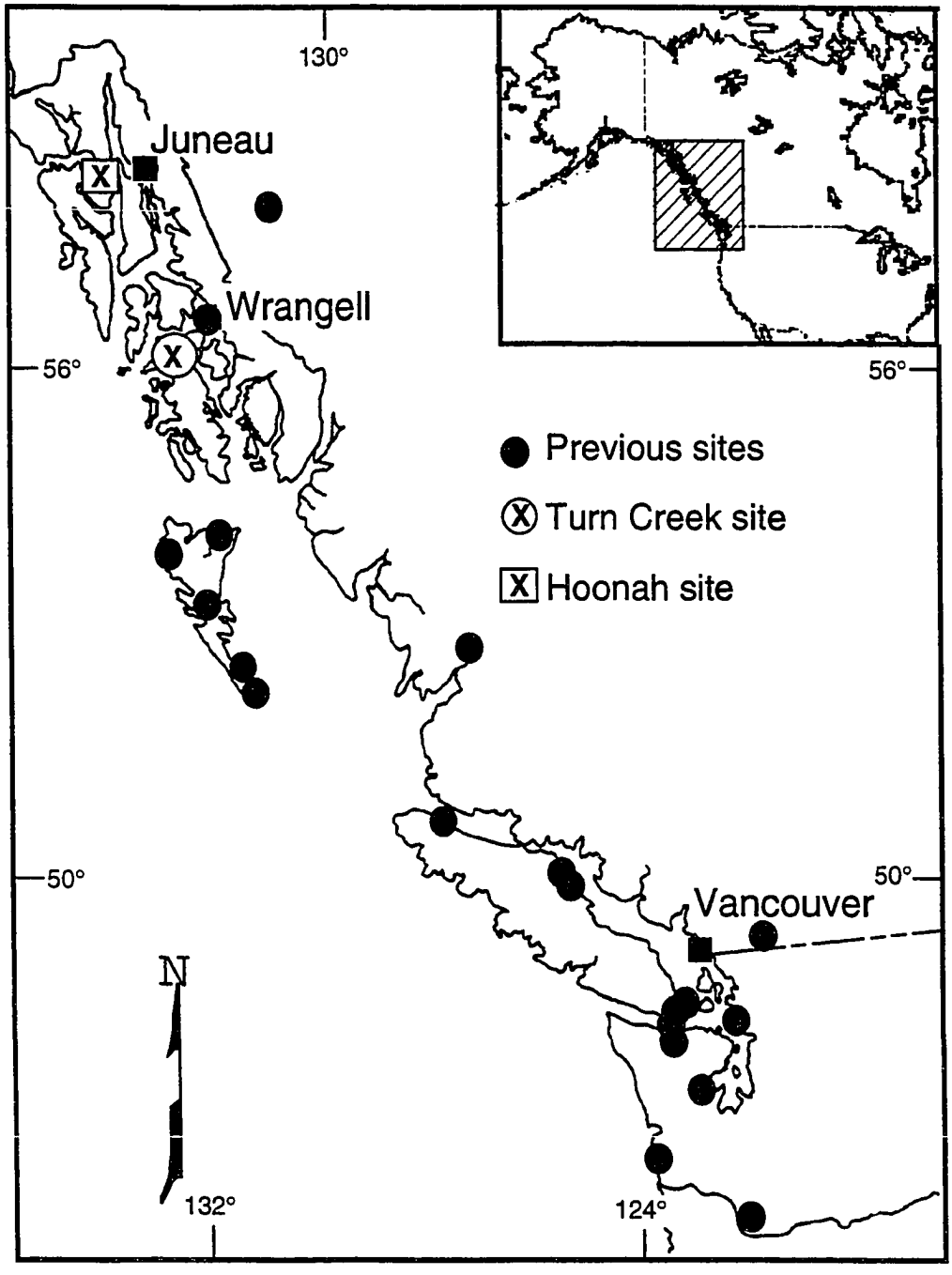


Figure 3. Locality records of *Myotis keenii* in the Pacific Northwest. Adapted from data presented by van Zyll De Jong and Nagorsen (1994).

Table 1. Measurements (in mm) of new *Myotis keenii* specimens.

Measure	UAM 23338	UAM 29831
Skull length	14.93	14.38
Mastoid width	6.91	6.88
Interorbital width	3.81	3.88
orbital width at lacrimal foramina	4.45	4.75
Rostral width	2.44	2.50
Maxillary width at M3	5.64	5.80
Palatal width at P2	3.64	3.65
Maxillary width at I3	2.51	2.63
Maxillary tooth row length	5.68	5.63
Length of P4M3	3.89	3.98
Length of M2	1.24	1.26
Width of M2	1.68	1.48
Upper canine width at cingulum	0.69	0.62
Total Body Length	88	86
Tail Length	39	35
Hind foot length	8	9
Ear length	17	15
Forearm length	37.28	35.35
Tibia length	17.00	16.08
Metacarpal 3 length	31.88	31.98
Metacarpal 5 length	31.64	29.66
Weight in grams.	6.0g	7.0g

Measurements are defined in van Zyll de Jong (1979).

stomach of the captured bat contained 40% trichoptera, 40% arachnida and 20% diptera. A second adult male *M. keenii* (UAM 29831) was collected on 11 July 1994 from a *M. lucifugus* maternity roost in the attic of an operating fish cannery at Hoonah on Chichagof Island (58° 06' N, 135° 26' W), approximately 160 km N of the Wrangell specimen (Figure 3). Body and cranial measurements for both specimens are summarized in Table 1.

The Turn Creek specimen was captured in a riparian area dominated by large western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*) with understory dominated by blueberry (*Vaccinium* spp.) and devil's club (*Oplopanax horridum*). The surrounding area is a mosaic of 13 habitat types that vary in dominant plant species, site productivity, and habitat structure (Table 2). I did not attempt to sample bats in all habitats. Bat activity, however, has been detected in highly productive forests (volume class 5 and 6), and occasionally in clearcut forests. Bats were rarely detected in second-growth forests 25-70 years old (volume class 4 and 5; Parker et al. *in press*). Specific habitat types were not available for the vicinity of the Hoonah capture site. This site is surrounded by large areas of clearcut and second-growth forest, as well as forested wetlands and riparian areas.

Discussion

While only three specimens of *M. keenii* have been recorded, little effort has been expended to investigate bat distribution in southeastern Alaska. I suggest that *M. keenii* is a resident throughout this region. *Myotis keenii* is nonmigratory, and these two recent specimens reinforce the occurrence of this species in southeastern Alaska. Further investigation, including the capture of female *M. keenii*, would further clarify status and range limits of this species in southeastern Alaska. Three other bat species, also known from few individuals, apparently reach the northwestern limits of their ranges in this region: the long-legged bat, *M. volans* (n = 5; Chapter 2; West 1993);

Table 2. Habitat types within 0.8 km of the Turn Creek capture location of *Myotis keenii* on Prince of Wales Island in southeastern Alaska.

Habitat Type	Dominant Vegetation[1]	Characteristics	Hectare
Forested Wetlands and Bogs	WH, YC, SP, BB, SC, SL	flat to broken slopes, low productivity, open stands, diverse structure, frequent snags	1110
Second-growth Forest (≥ 15 years)	WH	Vegetation depauperate, canopy closed	607
Moderate-High Productivity Forests	WH, RC, BB	Broken hillslopes, closed canopy	494
Clearcut Forests (< 15 years)	WH, RC, BB	Dense debris, vegetation not depauperate	260
Moderately Productive Forests	WH, RC, BB, SL	Dissected footslopes, alluvial fans, frequent snags	235
Riparian	SS, WH, AL, DC	0-15% slopes, floodplain, high productivity	97
Beach Forest	WH, lesser SS, RC, BB, SC	gravely beach, moderate productivity	76
Peatlands (Bogs & Fens)	stunted SP, Sphagnum, SD, LT, BK, SB	High (fens) or low (bog) productivity. Open habitat.	57
High Productivity Karst	WH, RC, BB	Smooth to dissected slopes, 50% canopy, well drained	54
Estuary	MH, SD	mudflats/estuaries	34
Moderate-High Productivity Forest	WH, RC, BB	Broken hillslopes, open canopy due to frequently blown down trees	20
Mixed Conifer	WH, SS YC, RC, BB, SC	moderate-low productivity, Open stands, diverse structure, frequent snags	17
Bare Ground	None	Bare rock and gravel	15

[1] Dominant vegetation as determined by methods described in DeMeo et al. 1992. AL = red alder (*Alnus rubra*), BB = blueberry (Vaccinium spp.), BK = bog kalmia (*Kalmia polifolia*), DC = devil's club(*Oplopanax horridum*), KB = Sitka burnet (*Sanguisorba sitchensis*), LT = Labrador tea (*Ledum groenlandicum*), MH = mountain hairgrass (*Deschampsia atropurpurea*), RC = red cedar (*Thuja plicata*), SB = salmonberry (*Rubus spectabilis*), SC = skunk cabbage (*Lysichitum americanum*), SD = sedges (Carex spp.), SL = salal (*Gaultheria shallon*), SP = shore pine (*Pinus contorta*), SS = Sitka spruce (*Picea sitchensis*), WH = western hemlock (*Tsuga heterophylla*).

California bat, *M. californicus* (n = 5; Chapter 2); and the silver-haired bat, *Lasionycteris noctivagans* (n = 4; Chapter 2). Only the little brown bat (*M. lucifugus*) is known from 185 specimens collected throughout the southeastern Alaska mainland and Alexander Archipelago (Chapter 2). These data suggest that *M. keenii*, as well as the other species mentioned are less abundant than *M. lucifugus* in southeastern Alaska.

The importance of southeastern Alaska's temperate rainforests to wildlife, including Sitka black-tailed deer (*odocoileus heminonus sitkensis*, Kirchhoff et al. 1983), river otter (*lutra canadensis*, Larsen 1983), bald eagles (*Haliaeetus leucocephalus*, King et al. 1972), Vancouver Canada geese (*Branta canadensis fulva*, Lebeda and Ratti 1983), and cavity nesting birds (Kessler 1979) has been established. Southeastern Alaska's temperate rainforests contain abundant live trees, snags, and fallen logs in a variety of sizes (Alaback 1991). Such structural diversity provides loose bark and tree hollows suitable for cavity-roosting species (Bunnell and Allaye-Chan 1984) such as bats (Barclay and Cash 1985; Christy and West 1993; Bradshaw *in press*; Vonhof *in press*). Greater use by bats of old-growth forests over second-growth and clearcut areas has been documented in British Columbia, Washington, and Oregon (Barclay and Cash 1985; Lunde and Harestad 1986; Thomas 1988; Christy and West 1993; Bradshaw *in press*; Vonhof *in press*), as well as in southeastern Alaska (Parker et al. *in press*). This suggests that temperate rainforests in southeastern Alaska provide important structure for *M. keenii* and other bat species.

Caves and crevices are also important bat habitat (Hill and Smith 1984), and over 1,769 km^2 of cave and crevice-containing karst occurs throughout southeastern Alaska (United States Department of Agriculture *in press*). The region is unique in its large number and high diversity of caves found in a high-latitude archipelago (Baichtal 1995). Because some of the most productive forests in southeastern Alaska are on karst (Baichtal 1995), this component of the Alexander Archipelago's rainforest ecosystem should be especially important bat habitat, providing forest and cave roosts, as well as

foraging habitat. The study of bat activity described in Chapter 4 indicates that such old-growth and riparian forests in southeastern Alaska are important foraging areas.

Although limited, data presented in this paper represent the only diet information available for *M. keenii*. The high percentage of flying insects (60%) and nonflying spiders (40%) consumed by this bat suggests that *M. keenii* has a flexible foraging strategy. Similar foraging behavior has been noted for *M. evotis* (Barclay 1991; Faure and Barclay 1994), a closely related species (van Zyll de Jong and Nagorsen 1994). These inferences are limited, however, because bat diets tend to change with season and relative abundance of different prey species (Buchler 1976; Fenton and Morris 1976; Anthony and Kunz 1977).

The Turn Creek bat was captured in a riparian area, and its stomach contained a high percentage of trichoptera, an aquatic insect. Other prey of this specimen occur throughout old-growth forests and riparian areas. These data imply that *M. keenii* forages in old-growth forests and riparian zones. Moreover, the variety of habitats near this site suggest the possibility that the surrounding area also provides foraging opportunities in clearcuts, forested wetlands, and other habitats. Further study of *M. keenii* ecology may help determine which habitats are important for this species.

The capture of the Hoonah specimen indicates that this species will at least occasionally roost in man-made structures with other species. Roost-sharing with other species occurs on Hot Spring Island in the Queen Charlotte Islands of British Columbia, where a colony of *M. keenii* roosts in association with *M. lucifugus* under rocks heated by a hot spring. Bats at the Hot Spring Island colony must abandon their roost periodically when it floods at high tide (Firman et al. 1993). It is uncertain whether this observation reflects this species' tolerance of disturbance, or lack of alternate, undisturbed warm roosts. Similarly, the Hoonah specimen may have been roosting in the noisy cannery due to lack of more suitable sites.

Forty-two percent of the most productive forests (timber volume classes 6 and 7) in southeastern Alaska were harvested by 1990 (United States Department of

Agriculture 1991; 1993), including over 70% of the karstland forests of Prince of Wales and neighboring islands (Baichtal 1995). Continued clearcut harvesting may alter forest structure important to bats (Thomas 1988). In fact, bat activity is rare in second-growth forests of southeastern Alaska (Chapter 4; Parker et al. *in press*). In view of the limited knowledge of *M. keenii* habitat requirements, its apparent affinity to old-growth coastal rainforests, and the extent of harvest of these forests in southeastern Alaska, further study of this species and its habitat requirements are warranted.

Chapter Four

Effects of Timber Harvest on Bat Activity in Southeastern Alaska's Temperate Rainforests

Abstract

Five bat species occur in southeastern Alaska's coniferous rainforests: *Myotis lucifugus, M. californicus, M. volans, M. keenii*, and *Lasionycteris noctivagans*. I compared bat activity in old-growth forests, riparian areas, closed-canopy second-growth forests, and clearcuts on Prince of Wales and Revillagigedo islands using ultrasonic bat detectors. Bats foraged in riparian areas and activity patterns in this habitat differed during lactation and post-lactation. Bat echolocation calls detected in old-growth forests consisted primarily of commuting activity. Bats fed in clearcuts, but activity was low. Bat activity in second-growth was very low. Activity levels and nightly activity patterns make it clear that conservation of old-growth forests and riparian areas is essential for continued viability of the southeastern Alaska bat community. Diet and reproduction of *M. lucifugus* in these temperate rainforests differed from that reported for conspecifics at lower latitudes. Preliminary information on diet for *M. keenii* and *M. volans* in southeastern Alaska is also presented. Over 300 caves have been surveyed in southeastern Alaska's 1,769 km^2 of karst terrain. Evidence of bats occupying these caves is widespread and seasonality of that occupation is just beginning to be assessed. I provide evidence that clearcuts and second-growth forests are used infrequently by bats in southeastern Alaska during summer. This study also provides evidence that old-growth forests and riparian zones are used often by bats.

Introduction

Microchiropteran bats are long-lived nocturnal insectivores with low reproductive rates and noncyclic populations (Findley 1993). These characteristics allow bats to achieve constant population levels in stable habitats, but may make them vulnerable when habitat is modified. Many populations of bats have suffered decline, and some are threatened or endangered (Tuttle 1979; Lowe et al. 1990; Speakman et al. 1991), due in part to habitat alteration (Lowe et al. 1990; Adam et al. 1994). The bat community of southeastern Alaska consists of five species. Four species, *Myotis californicus, M. volans, M. keenii,* and *Lasionycteris noctivagans* reach the northern limit of their range in southeastern Alaska. The fifth, *M. lucifugus,* is the most commonly encountered species of bat in southeastern Alaska, and also occurs in more northerly parts of Alaska and Canada (Chapter 2; Youngman 1975; Hall 1981).

Over 42% of the most productive forests (timber volume classes 6 and 7) in southeastern Alaska had been harvested by 1990 (United States Department of Agriculture 1991; 1993), and extensive harvest of timber continues (United States Department of Agriculture *in press*). To test whether timber harvest affects the use of these forests by bats, I compared relative levels of bat activity in high volume (volume class 5 and 6) old-growth forests, riparian areas, clearcuts, and closed-canopy second-growth forests. To test whether activity of bats in old-growth forests and riparian areas differed between July and August or between habitat types, I analyzed the nightly pattern of bat activity and relative feeding activity in these habitats. To provide a baseline for future studies on bat ecology in southeastern Alaska, I collected preliminary data on bat diets, reproduction in *M. lucifugus,* and seasonal occupation of caves.

Methods

Study Area

This study was conducted in southeastern Alaska from 29 May through 28 August 1993. Southeastern Alaska is the wettest and coldest part of the coniferous rainforests of the north-temperate zone (Walter 1985). This ecosystem stretches from 54° to 60° N latitude, and includes the Alexander Archipelago and a narrow strip of mainland coast. The coastal mountain range and glacier fields isolate the region geographically and climatologically from nearby British Columbia and southcentral Alaska (Figure 4).

Study sites were on northern, central, and southeastern Prince of Wales and western Revillagigedo islands at 55° to 56° N latitude (Figure 5). Prince of Wales, the third largest island in the United States, covers 4,557 km^2. Karst topography is well developed over much of northern and central Prince of Wales Island. This karst landscape has many caves and crevices and contains some of the most productive forests on the island (Aley et al. 1993). Study sites were on harvested and unharvested areas of karst and noncarbonate lands (Table 3). Revillagigedo Island is approximately one-half the size of Prince of Wales Island and has little karst. Study sites on this island were on noncarbonate terrain. Heavy rains occur in all seasons throughout the study area. Annual precipitation varies from 4,064 mm on western Revillagigedo Island to 2,032 mm on northern Prince of Wales Island (Hartman and Johnson 1978).

Forest Habitats Monitored

Habitat investigated were: 1) old-growth forests dominated by western hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), and red cedar (*Thuja plicata*), 2) riparian areas (edge of streams or ponds 10-25 m wide; Table 3) within these forests, 3) closed-canopy second-growth forests harvested 25-70 years ago, and 4) forests clearcut harvested 5-17 years ago in which the canopy had not yet closed. Six sites in each of

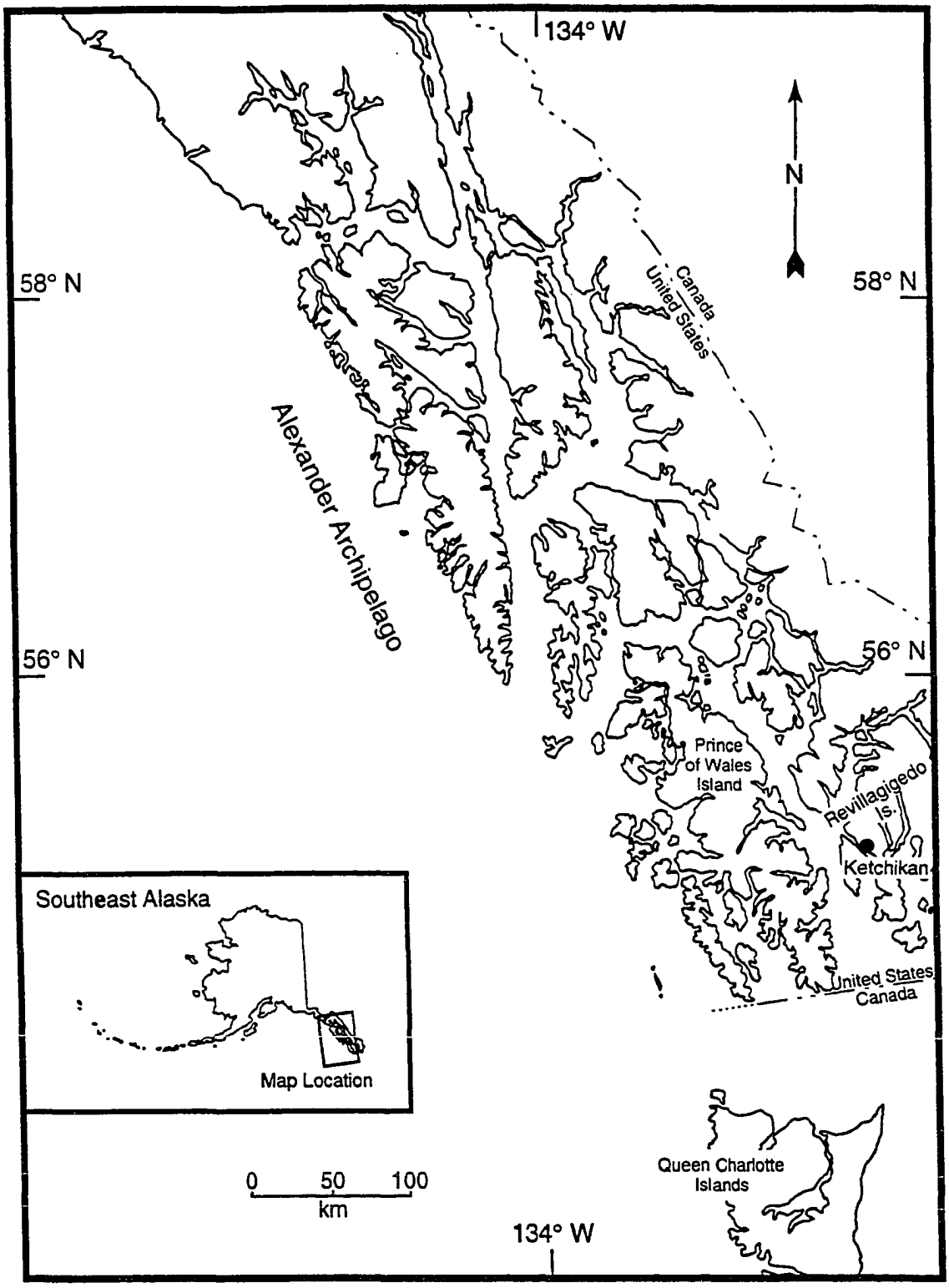


Figure 4. Southeastern Alaska

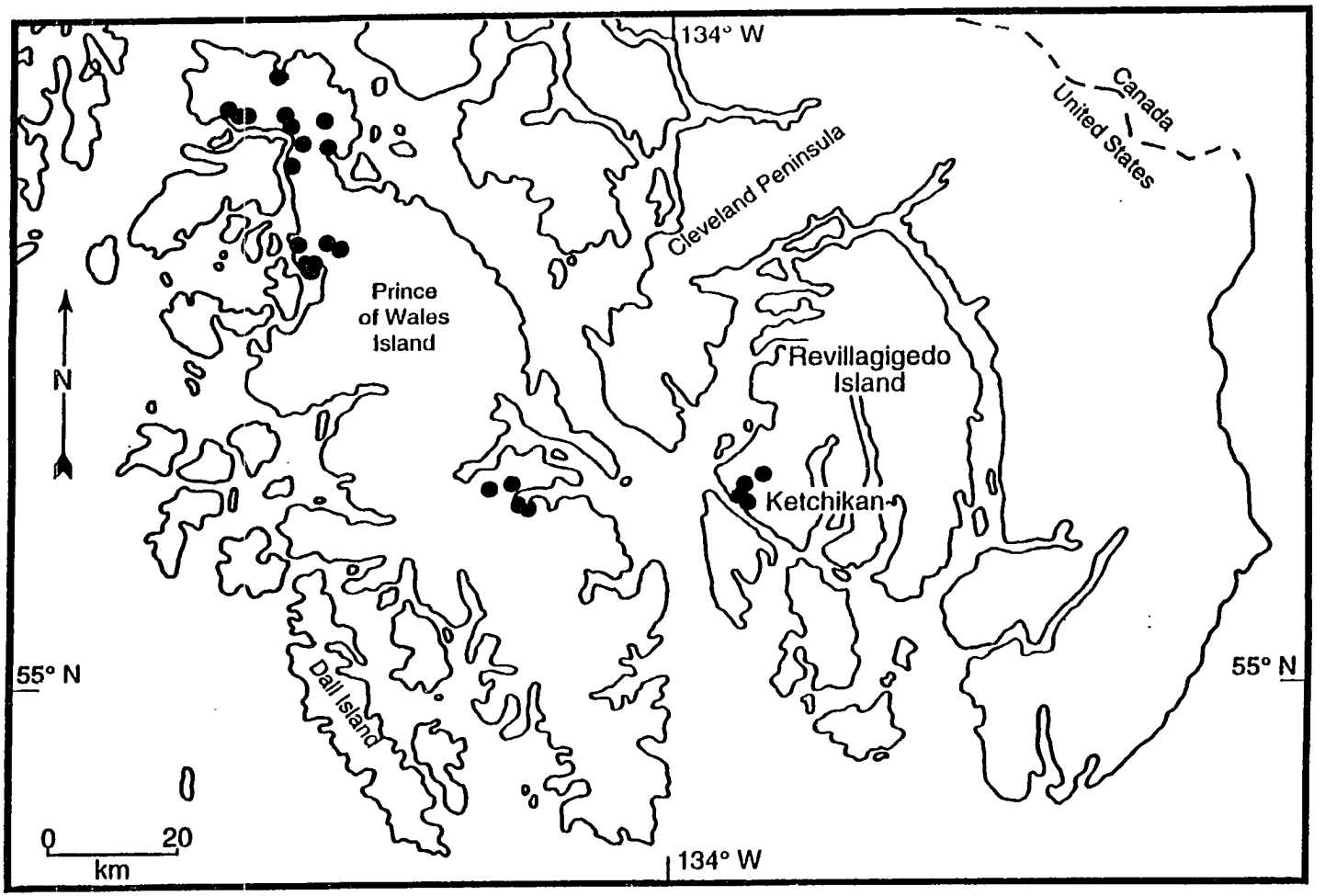


Figure 5. Study sites on Prince of Wales and Revillagigedo Islands.

Table 3. Vegetation characteristics and karst at study sites, as determined by sampling a 20 by 40 m plot at each site.

Site Type	Karst	Overstory Species[1]	Understory Species[1]	Canopy Height[2]	No. Trees[3]	No. Snags[4]	Stream Width	Grad
Riparian Sites								
Red Creek	no	WH/SS	Vacc/DC	24 m	28	7	20 m	2%
Turn Creek	yes	WH/SS	Vacc	27 m	26	2	10 m	2%
108 Creek	no	WH/SS	Vacc/SC	34 m	7	6	18 m	2%
Yatuk Creek	yes	WH/SS	DC/SB	37 m	12	1	10 m	2%
Polk Creek	no	WH/RC	Vacc/SL	31 m	23	14	25 m	4%
Frog Pond	no	SP	CB	7 m	10	0	15 m	0%
mean				26.67	17.67	5	16.33	2
Standard error				4.37	3.69	2.13	2.39	0.51
Old-growth Sites								
Calder	yes	WH/RC	Vacc/SF	31 m	34	9		
Beaver Falls	yes	WH/SS	Vacc/DC	33 m	33	5		
River's End	yes	WH	Vacc/DC	34 m	15	7		
Sarkar	no	WH	Vacc	34 m	18	2		
Polk	no	WH	Vacc/DC	31 m	28	7		
Perseverance	no	WH/RC	Vacc/SC	30 m	31	6		
mean				32.17	26.5	6		
Standard error				0.7	3.29	0.97		
Clearcut Sites								
Calder	yes	WH/SS[5]	Vacc	5 m	0	0		
Roaring Road	yes	WH[5]	Vacc/DC	2 m	0	0		
Naukati	yes	WH/SS[5]	Vacc	1 m	0	0		
Yatuk	no	WH[5]	Vacc	3 m	0	0		
Polk	no	WH[5]	Vacc	2 m	0	0		
Ketchikan	no	WH[5]	Vacc/SC	2 m	0	0		
mean				2.5	0	0		
Standard error				0.56	0	0		
Second-growth Sites								
Calder	yes	WH/SS	Vacc	18 m	86	1		
Starlight	yes	WH/SS	Vacc/DC	10 m	37[6]	1		
Naukati-1	yes	WH/SS	Vacc	18 m	110	2		
Naukati-2	yes	WH/SS	Vacc	18 m	104	2		
Polk	no	WH/SS	Vacc/DC	17 m	52	0		
Pipeline	no	WH	Vacc/DC	12 m	60	1		
mean				15.5	74.83	1.17		
Standard error				1.45	12.09	0.31		

[1] Determined by methods described in DeMeo et al. 1992. WH = *Tsuga heterophylla* (western hemlock), SS = *Picea sitchensis* (Sitka spruce), RC = *Thuja plicata* (red cedar), SP = *Pinus contorta* (shore pine), Vacc = *vaccinium alaskaense/ovalifolium* (blueberry species), DC = *Oplopanax horridum* (devil's club), SC = *Lysichitum americanum* (skunk cabbage), SL = *Gaultheria shallon* (salal), SF = *Polysticum munitum* (swordfern), SB = *Rubus spectabilis* (salmonberry), CB = *Empetrum nigrum* (crowberry).
[2] Average canopy height of overstory trees in riparian, old-growth, and second-growth. Average height of young trees in clearcuts.
[3] Number of trees ≥ 12 cm DBH (diameter at breast height).
[4] Number of dead trees ≥ 12 cm DBH and ≥ 2 m tall.
[5] Tree species before harvest.
[6] Site thinned in mid 1980's.

the four habitat types were monitored. The 24 study sites were ≥ 16 ha at elevations ≤ 250 m. Dominant overstory (tree) and understory (shrub and herb) species at each study site (Table 3; DeMeo et al. 1992) were described. To ensure within-habitat uniformity, I estimated overstory height with a clinometer and tape to the nearest 1 m, and quantified trees and snags within a 20 by 40 m area at each site. Multiway analysis of variance (MANOVA) was performed to determine whether there were significant differences among the four habitat types ($P \leq 0.05$; Zar 1984). Variables in the MANOVA were: presence/absence of karst, canopy height, number of trees per 20 by 40 m plot, and number of snags per plot. Tukey pairwise comparisons were also performed to determine whether canopy height, number of trees per plot, and number of snags per plot differed among habitats ($P < 0.05$; Zar 1984).

Activity Levels and Types of Calls

To determine relative levels of bat activity among habitat types, echolocation calls were recorded with countdown mode bat detectors and delay switches (Anabat II, Titley Electronics, Ballina N. S. W., Australia) attached to voice activated cassette-tape recorders (Radio Shack Realistic Minisette 20). A single bat call was defined as ≥ 2 ultrasonic pulses (Griffin 1958) detected from the time the bat detector began recording calls until the calls were no longer audible. The time of each call was recorded automatically. The electronic equipment was placed in a plastic box with a hole cut out for the microphone and a 3-cm roof was attached to shelter the microphone from rain. A light sensor turned the system on at dusk and off at dawn. One bat detector was placed in each site at least 90 m from the habitat edge and approximately 2 m above the ground. To reduce the possibility that different weather conditions on different nights would affect the results, each habitat type was monitored every night. All 24 sites were monitored ultrasonically for 1 to 9 nights (average 4.6).

Echolocation calls of bats were transcribed from the recordings and grouped in 5-min intervals. Anabat II Bat Call Analysis software version 1.1 (Titley Electronics,

Ballina N. S. W., Australia) was used to display call sonograms to determine whether questionable sounds were bat calls or extraneous noise (e.g., raindrops). I could not unequivocally differentiate the species of *Myotis* by their calls because of the similarity of calls of the species inhabiting southeastern Alaska (Thomas et al. 1987; Thomas 1988). To test for differences in the proportion of nights with bat activity, I performed χ^2 tests of independence (Zar 1984). A feeding buzz was defined as an increased pulse repetition rate which, to the human ear, blended the calls together into a buzz (Griffin 1958). To test for differences in the proportion of calls containing feeding buzzes, I performed χ^2 tests of independence (Zar 1984) of all calls from old-growth, clearcuts, and second-growth. In riparian sites, a sample of 2,035 calls were used in the χ^2 tests for calls containing feeding buzzes. These echolocation calls were recorded on 25 different nights at all six riparian sites. Four nights of data in riparian sites were left out of the analysis of feeding buzzes because those recordings were difficult to access and an adequate sample size was reached. Because bat calls were not normally distributed and variances were not equal among habitats, Kruskal-Wallis one-way analysis of variance was used to compare average calls per night among habitat types.

Activity Patterns

To test whether nightly patterns of activity differed between habitat types or temporally, I compared nightly patterns of call activity during the periods 14-21 July and 17-28 August. Night length in southeastern Alaska varies from 6 h 32 min on 21 June to 11 h 9 min on 31 August. This could affect activity patterns as the night lengthens throughout summer. Additionally, energy demand in *M. lucifugus* (Kurta et al. 1987) and foraging activity patterns of other species (Swift 1980) change as female reproductive state changes during summer. Only old-growth forests and riparian sites had adequate bat activity for comparison ($\geq$ 8 consecutive nights of recorded activity and $\geq$ 100 calls during that period). To remove the bias of fewer calls at the end of the night due to the tape running out or battery failure, I calculated the average of calls-per-

5-min-interval, weighted by the number of intervals in which equipment was working. To smooth out peaks and make it easier to detect patterns in the data, I used a moving average of 5 intervals. Time from sunset to sunrise increased from 7 h 6 min to 9 h 58 min between 14 July and 28 August. Length of twilight decreased from 48 min (13 percent of the night) to 18 min (three percent of the night), and no bats were detected before sunset or after sunrise. Therefore, I compared intervals beginning at sunset, rather than using clock time. Activity that occurred later than 7 h 9 min after sunset (i.e., sunrise on 14 July) was excluded from comparison, due to the ambiguity of comparing bat activity during this nighttime period in August to a time period which is after sunrise during much of July. Resulting patterns were compared using Kolmogorov-Smirnov goodness of fit tests for cumulative data (Zar 1984). Because of the small data set, I tested only whether overall patterns differed and did not statistically compare portions of the night.

Prey items

Sixteen *M. lucifugus*, one *M. keenii*, and one *M. volans* were collected with mist nets placed over streams in the study area (Chapters 2 and 3; Parker and Cook *in press*). Stomachs were preserved in 70% ethanol. Stomach contents were classified to order or family by J. O. Whitaker, Jr., Indiana State University, who also estimated percent volume and percent frequency of each food category.

Results

Forest Habitat Comparisons

Multiway analysis of variance determined that there were significant structural differences among the four habitat types ($P < 0.05$; Zar 1984). Tukey pairwise comparisons determined that canopy height and number of trees per plot did not differ between riparian and old-growth habitats, but did differ from clearcut and second-growth habitats (Table 4; $P \leq 0.05$; Zar 1984). Canopy height and number of trees per

plot also differed significantly between clearcut and second-growth sites (Table 4; $P \leq 0.05$; Zar 1984). Number of snags per plot was significantly different between riparian and clearcut sites, between old-growth and clearcut sites, and between old-growth and second-growth sites. There was no significant difference in number of snags per plot between riparian and old-growth sites, riparian and second-growth sites, or between clearcut and second-growth sites (Table 4; $P \leq 0.05$; Zar 1984). Sample size was too small to determine within-habitat differences between karst and nonkarst sites.

Table 4. Tukey pairwise comparisons of habitat characteristic means ($P \leq 0.05$).

Habitat Type	Stand height*	Number of trees*	Number of snags*
riparian	A	A	AB
old-growth	A	A	A
clearcut	B	B	C
second-growth	C	C	BC

* Means with the same letter are not significantly different.

Activity Levels and Call Type

One hundred thirteen plot-nights of sampling yielded 2,716 bat echolocation calls. There were 2,508 bat calls detected in riparian habitat during 29 nights sampled; 150 calls in old-growth during 25 nights; one call in second-growth during 30 nights; and 57 calls in clearcuts during 29 nights (Table 5). In addition to echolocation calls listed above, bats were detected on two additional nights in riparian sites, but the

number of calls could not be determined. These nights were only used to compare the proportion of nights with bat activity. Proportion of nights with bat activity ($\geq$ 1 call per night) differed significantly among the four habitats ($\chi^2 = 33.04$, $P \leq 0.05$). Pairwise comparisons showed no significant difference in number of nights with activity in riparian and old-growth ($\chi^2 = 0.71$, $P \geq 0.05$). There were significantly more nights with activity in old-growth than in clearcuts ($\chi^2 = 6.29$, $P \leq 0.05$), and in clearcuts than second-growth ($\chi^2 = 5.70$, $P \leq 0.05$).

Average number of calls per night among the four habitats was significantly different ($H = 68.27$, $P \leq 0.0001$). Multiple comparisons showed significant differences between riparian and old-growth ($H = 3.40$, $P \leq 0.05$), and old-growth and second-growth forests ($H = 3.82$, $P \leq 0.05$). Differences between average calls per night in old-growth and clearcuts were not significant ($H = 2.48$, $P \geq 0.05$). Nonetheless, 47 of the 57 calls in clearcuts occurred during the night of 5 July, 37 of those within a 30 min period. There was no significant difference in average calls per night between clearcuts and second-growth forests ($H = 1.40$, $P \geq 0.05$) . In riparian sites, a sample of 2,035 calls (25 nights) revealed that 356 contained feeding buzzes, whereas in old-growth, 6 of 150 calls contained feeding buzzes. In clearcuts, 6 of 57 calls contained feeding buzzes, 5 of these were among the 47 calls detected on 5 July. The single call in second-growth did not contain a feeding buzz. There was a significant difference in proportion of calls that contained feeding buzzes among riparian, old-growth, and clearcut habitats ($\chi^2 = 11.97$, $P \leq 0.05$). Pairwise comparisons showed significant differences between riparian and old-growth ($\chi^2 = 11.54$, $P \leq 0.05$), but not between clearcuts and riparian (Table 5; $\chi^2 = 0.734$, $P \geq 0.05$), or between clearcuts and old-growth ($\chi^2 = 3.05$, $P \geq 0.05$).

Table 5. Bat activity in forest habitats.

Habitat Type	Number of nights sampled	Total number of calls	Average calls per night*	Percent nights with bat activity*	Percent calls with feeding buzz*
Riparian	29+2[†]	2508**	86 ± 17.01 A	94 A	17.5 A
Old-growth	25	150	6 ± 2.03 B	76 A	4 B
Clearcuts	29	57	2 ± 0.37 B	28 B	10.5 AB
Second-growth	30	1	0.03 ± 0.03 C	3 C	0
Total	113	2716			

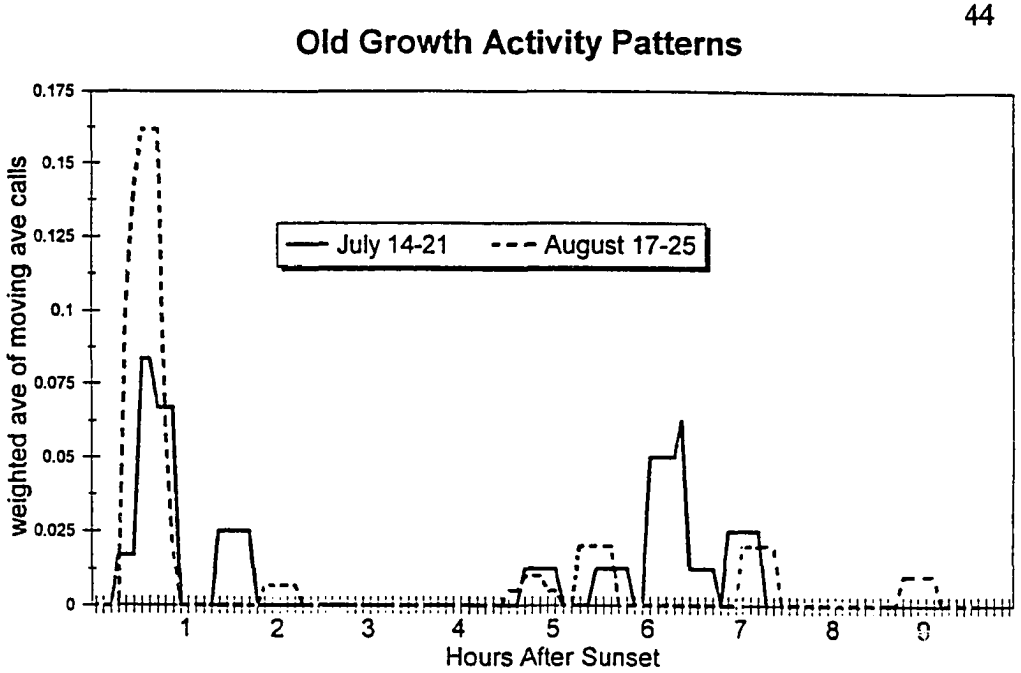
* Items with the same letter are not significantly different ($P < 0.05$).

** A sample of 2035 calls representing data from 25 nights were used to compare the number of calls containing feeding buzzes. See methods for explanation.

[†] 29 nights were used to calculate percent of total calls and average calls per night, 31 nights were used to calculate percent nights with bat activity. See methods for explanation.

Activity Patterns

Calls were not detected before sunset or after sunrise in any habitat during the study period (Figure 6). Activity patterns differed significantly between old-growth and riparian habitat in July ($D = 0.205$, $DF = 88$, $P \leq 0.001$); in August between old-growth and riparian habitats ($D = 0.172$, $DF = 126$, $P \leq 0.001$); and in riparian habitat between July and August ($D = 0.205$, $DF = 88$, $P \leq 0.001$). There was no significant difference between July and August activity patterns in old-growth ($D = 0.138$, $DF = 94$, $P > 0.05$). Bat activity in riparian areas began 15-20 min after sunset during both July and



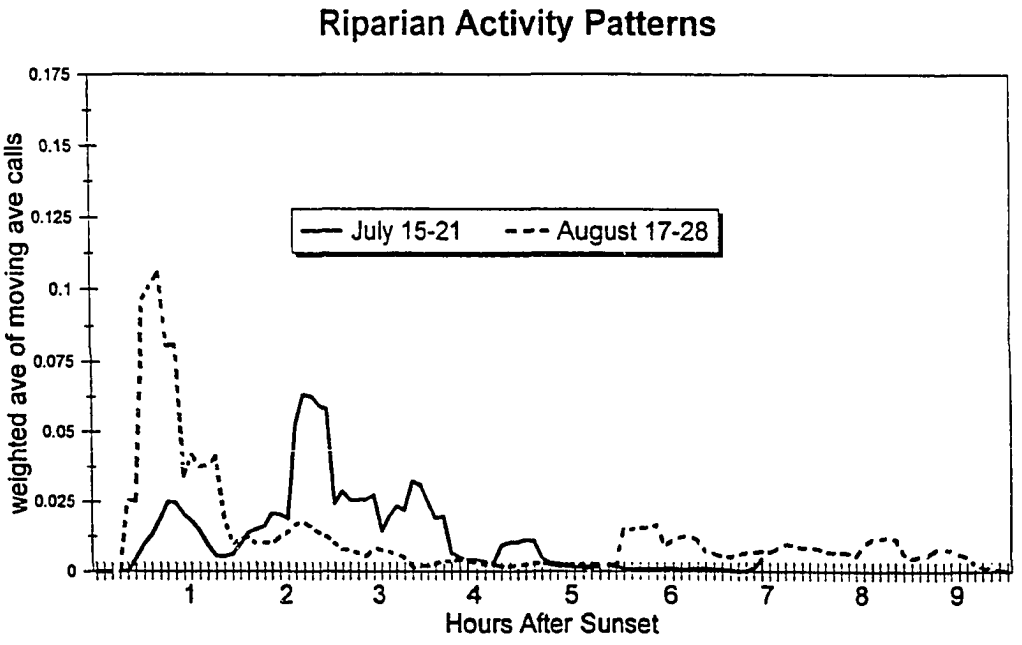


Figure 6. Activity patterns of bats in riparian and old-growth sites during July and August.

August. In July there were two additional activity peaks within 4 h of sunset and almost no activity during the next 3 h before sunrise. In August, activity was low throughout the remainder of the night, even though the night was longer and twilight was shorter.

Prey Items

Percent volume and percent frequency of prey consumed by the 16 *M. lucifugus*, 1 *M. volans*, and 1 *M. keenii* represented a variety of taxa (Table 6). The frequent occurrence of spiders (Aranea) is noteworthy because they are an unusual prey source.

Table 6. Volume and frequency of prey items in stomach contents.

	Myotis lucifugus n = 16		*Myotis volans* n = 1	*Myotis keenii* n = 1
Prey	**% Vol.**	**% Freq.**	**% Vol.**	**% Vol.**
Chironomidae	50.0	69.0	20.0	---
Diptera	24.4	50.0	50.0	20.0
Araneae	15.4	33.3	5.0	40.0
Trichoptera	4.4	6.3	---	40.0
Tipulidae	2.2	6.3	---	---
Lepidoptera	1.3	6.3	---	---
Phoridae	0.6	6.3	---	---
Coleoptera	0.6	6.3	---	---
Ephemerida	0.6	6.3	---	---
Culicidae	0.6	6.3	---	---
Nycteribiidae	---	---	20.0	---
Formicidae	---	---	5.0	---

Discussion

Riparian Areas

Riparian habitat had the highest proportion of nights in which bats were detected, highest number of bat calls per night, and the highest proportion of calls containing feeding buzzes. Among the four habitats sampled, riparian areas were the most important foraging sites for bats. The importance of riparian areas as feeding habitat has been frequently noted at lower latitudes and drier climates (Buchler 1976; Fenton and Bell 1979; Bell 1980; Nagorsen and Brigham 1993). *Myotis lucifugus*, the most commonly encountered species in southeastern Alaska (Chapter 2), tends to circle when foraging (Fenton and Bell 1979; Fenton et al. 1980). The higher number of bat detected per night may have been influenced by individual bats being detected multiple times as they foraged. Nevertheless, the higher proportion of nights that bats were detected in riparian habitat and the high proportion of calls containing feeding buzzes in these sites support the conclusion that riparian areas are important bat habitat.

The temporal change in activity patterns in riparian areas likely reflects seasonal changes in energy needs at this high latitude. I suggest that the prolonged foraging activity in July is in response to the high energy demand of lactation and the subsequent need to forage longer. Chapter two indicates that lactating females in southeastern Alaska were captured before 1 August, and no lactating females were captured after that date. This suggests that 14-21 July is within the lactation period for *M. lucifugus*, and 17-28 August is post-lactation. The temporal activity of bats in this study corroborates other studies that reported female *M. lucifugus* foraged up to 4 h/night during late pregnancy and lactation (Kurta et al. 1989), and forage several times per night, returning to the maternity roost between foraging bouts to nurse their young (Anthony and Kunz 1977; Anthony et al. 1981). By mid-August, females no longer have the high energy demand of lactation (Kurta et al. 1987), and can meet energy needs in a shorter period

of time (Anthony and Kunz 1977). This is reflected by the August activity pattern, in which most activity occurred within 2 h of sunset. Insect availability is low during the latter part of the night (Anthony and Kunz 1977; Barclay 1991) and probably makes foraging less efficient than conserving energy (Pulliam 1981) by roosting. Foraging juveniles may account for the low activity level during the remaining 8 h before sunrise in August. Juveniles are less adept at capturing insects, and must forage longer to meet energy needs (Anthony and Kunz 1977). A similar change in foraging patterns was noted for *Pipistrellus pipistrellus* at 57° N latitude in Scotland. During lactation these bats foraged just after sunset and again prior to sunrise. During pregnancy and post-lactation they foraged only once, immediately following sunset (Swift 1980). In contrast to my study, Anthony et al. (1981) noted that *M. lucifugus* in New Hampshire had a bi-modal pattern of foraging activity throughout summer. Differences in study methods may be responsible for differences observed between this study and *M. lucifugus* in New Hampshire. I monitored echolocation calls in riparian habitat, whereas Anthony et al. (1981) monitored bats leaving and entering night roosts.

An alternative theory to female reproductive condition influencing these nightly activity patterns is the possibility of differing prey availability between these two time periods. This possibility should also be investigated.

Old-growth Forests

Old-growth was the habitat with the second highest bat activity. Even though old-growth sites had fewer average calls per night than riparian sites, calls were heard during 76% of nights monitored. This regular occurrence of bats suggests that it is important for summer roosts. Temperate rainforests of southeastern Alaska contain abundant live trees, snags, and fallen logs in a variety of sizes (Alaback 1991). Such structural diversity provides suitable sites for cavity-roosting species (Bunnell and Allaye-Chan 1984) such as bats (Barclay and Cash 1985; Christy and West 1993). Use of old-growth forests by bats for roosting and foraging has been documented in British

Columbia, Washington, and Oregon (Barclay and Cash 1985; Lunde and Harestad 1986; Thomas 1988; Christy and West 1993; Bradshaw *in press*; Vonhof *in press*). Bat roosts and foraging sites are likely to occur throughout old-growth forests, dispersing bats and decreasing the likelihood of a bat passing by an ultrasonic detector placed randomly in the forest. In addition, because bats in old-growth sites appeared to be primarily commuting, they were not likely to pass the bat detector more than once. The six calls with feeding buzzes in old-growth indicate that foraging also occurred in this habitat. All bat species in southeastern Alaska likely forage in old-growth forests (Saunders and Barclay 1992; Nagorsen and Brigham 1993; van Zyll de Jong and Nagorsen 1994), especially *M. keenii* (Parker and Cook *in press*). Nightly activity in old-growth forests remained the same in July and August. This predominantly commuting activity was highest immediately following sunset when bats left their roosts to travel to foraging sites. A few bats were detected at different intervals throughout the rest of the night, and may have been bats returning to day roosts.

Old-growth forests in southeastern Alaska may be important to bats primarily for roosting sites. Too little is known about the ecology of bats in these temperate rainforests to be sure that they are not equally important as foraging areas for species such as *M. keenii* (Parker and Cook *in press*). Availability of roost structure is an important factor limiting bat distribution and abundance in temperate climates (Humphrey 1975; Kunz 1982*a*). In other portions of their range, *Myotis lucifugus, M. volans, M. californicus, M. keenii*, and *L. noctivagans* roost under loose bark, in snags and hollow trees (Barclay and Cash 1985; Thomas 1988; Christy and West 1993 Bradshaw *in press*; Vonhof *in press*). In addition, extensive karst formations in southeastern Alaska (Buddington and Chapin 1929; Aley et al. 1993; Baichtal 1995) provide numerous caves and crevices where hibernating bats have been observed (Chapter 2).

Clearcut Forests

The smaller proportion of nights in which bats were detected in clearcuts than in old-growth indicates that bat activity in old-growth was more consistent than in clearcuts. This is likely due to the lack of roost structure in clearcuts. Current methods of clearcutting timber in southeastern Alaska eliminates snags, decaying trees, and large trees with loose bark (Cline et al. 1980), thereby eliminating roost sites.

Insectivorous bats will exploit patches of insects (Belwood and Fenton 1976; Bell 1980), and this is apparently what at least one bat was doing in the clearcut that showed unusually high bat activity on 5 July. Activity on that night also influenced the lack of statistical significance in the average calls per night between clearcuts and old-growth forests or riparian habitats. Clearcuts in southeastern Alaska may be used occasionally by *L. noctivagans* and *M. volans*, which sometimes forage in open areas (Fenton and Bell 1979; Nagorsen and Brigham 1993).

Second-growth Forests

The high density of even-sized, closely spaced trees, and the lack of snags and decaying trees in second-growth (Alaback 1984a; Bunnell and Allaye-Chan 1984) are likely reasons for the low activity by bats in this habitat. In southeastern Alaska, old-growth characteristics, including the structural diversity needed for bat roosts, begin to develop 150-200 years after harvest (Alaback 1984*b*). Perhaps bats foraged above the second-growth canopy and were not detected because the dense canopy blocked echolocation calls. The single echolocation call recorded in second-growth indicates that it is possible to detect calls in this habitat. More calls should have been recorded if bats foraged above the second-growth canopy. In a similar study in the Pacific Northwest, bats were detected three to ten times less often in second-growth than in old-growth forests, even when bat detectors were placed in the tree canopy as well as on the ground (Thomas 1988). My study indicates that little bat activity occurs in second-growth forests of southeastern Alaska.

Bat Ecology

The ecology of bat species in southeastern Alaska has been extrapolated from knowledge of the habits of these species at lower latitudes, even though four species reach their latitudinal limits in these temperate rainforests (Chapter 2). My data represent the only diet information for *M. lucifugus, M. keenii* and *M. volans* in southeastern Alaska. Much of the prey consumed by the 16 *M. lucifugus* collected in this study were similar to that of *M. lucifugus* elsewhere in North America (Whitaker 1972; Buchler 1976; Whitaker et al. 1977; Whitaker et al. 1981). The wide range of prey suggests that *M. lucifugus* feeds opportunistically in southeastern Alaska, as it does elsewhere (Belwood and Fenton 1976; Anthony and Kunz 1977; Fenton and Barclay 1980). The consumption of spiders, however, has been noted only at higher latitudes in Alaska (Whitaker and Lawhead 1992). While *M. lucifugus* seldom gleans insects from foliage, (Fenton et al. 1980; Barclay 1991), it commonly plucks insects from water (von Frenckell and Barclay 1987; Barclay 1991). Prolonged rainstorms may cause *M. lucifugus* to seek prey inside caves (personal observation) and in the shelter of overhanging cliffs. Why or how *M. lucifugus* preys on spiders in the rainforests of southeastern Alaska, but not at lower latitudes remains unanswered.

The diet of a single *M. keenii* specimen should be interpreted with caution because prey consumed by bats tends to change with season and insect abundance (Buchler 1976; Fenton and Morris 1976; Anthony and Kunz 1977). Nevertheless, my information are the only data available for *M. keenii*. The diet of this specimen, which consisted of 60% flying insects and 40% non-flying spiders suggests that *M. keenii* has a versatile foraging strategy (Parker and Cook *in press*). Diet of the single *M. volans* was similar to the combination of flying and nonflying prey reported in Oregon for this species (Whitaker et al. 1977; Whitaker et al. 1981).

Reproduction in *M. lucifugus* also appears to differ between southeastern Alaska and lower latitudes. At lower latitudes, in areas of high summer rainfall and low

ambient temperature, *M. lucifugus* has a low female:male ratio, and females are nonreproductive (Thomas 1988; Barclay 1991). Inclement weather may not allow sufficient time during the night for females to meet energy demands of pregnancy and lactation (Thomas 1988; Barclay 1991; Grindal et al. 1992). In southeastern Alaska however, the female:male ratio is equal and reproductive females have been captured (Chapter 2). This suggests that female *M. lucifugus* are able to meet the energy demands of pregnancy and lactation in southeastern Alaska rainforests, even though prolonged rainstorms are common. Changes in activity patterns between lactation and post-lactation support this conclusion. Consumption of over 15 percent nonflying prey, such as spiders (Whitaker and Lawhead 1992), may enable these bats to maintain a positive energy balance.

Conclusions

Federal law in the United States requires public land managers to inventory and maintain viable populations of wildlife affected by land management practices, such as timber harvest (United States Congress 1976). My study suggests that old-growth forests and riparian areas provide roosting and foraging habitat for bats in southeastern Alaska. The extent of past and future timber harvest in southeastern Alaska (United States Department of Agriculture 1991; 1993; *in press*) suggests a significant effect on these species. My data also indicate little bat activity in clearcuts, perhaps because clearcuts do not provide roosting structure. Bats occasionally fed on insect swarms in clearcuts. Closed-canopy second-growth is not used by bats in the rainforests of southeastern Alaska. Old-growth characteristics that provide suitable roost sites for bats do not develop until at least 150 years after harvest (Alaback 1984*b*), and current plans for the Tongass National Forest project a 150-year harvest rotation (United States Department of Agriculture 1991). Planning and environmental assessment processes for public lands should include information from this study when considering the effects of land management practices.

Southeastern Alaska is unique among high-latitude archipelagos because of its large number and high diversity of caves (Aley et al. 1993; Baichtal 1995). Over 1,769 km^2 of southeastern Alaska's 26,305 km^2 Tongass National Forest are on karst terrain (United States Department of Agriculture *in press*). Caves and crevices are also important bat habitat (Hill and Smith 1984). Personal observations suggest that bats occupy caves during cold spells in the winter, but leave these caves during warmer weather. Guano and skeletal remains have been observed in several caves. During eight summers of intensive mapping and exploration of more than 340 significant caves, no bats have been observed (S. W. Lewis and K. Allred *unpublished data*). Future studies should examine seasonal changes in roost selection to determine when bats in southeastern Alaska occupy forest and cave roosts. Studies should also assess what aspects of cave morphology create microclimates suitable for hibernating bats. Because some of the most productive forests in southeastern Alaska are on karst (Baichtal 1995), this component of the rainforest ecosystem in southeastern Alaska should be especially important bat habitat, providing forest and cave roosts, as well as foraging habitat. Documentation of winter activity patterns and foraging strategies in relation to weather patterns and habitat type will be important in determining the effects of timber harvest on bats.

My study provides evidence that the ecology of *M. lucifugus* in southeastern Alaska should not be extrapolated from studies of this species at lower latitudes. Reproduction and diet appear to differ between *M. lucifugus* in southeastern Alaska and conspecifics at lower latitudes. Why or how this species preys on spiders in southeastern Alaska but not at lower latitudes remains unanswered. Ecology of *M. volans*, *M. keenii*, *M. californicus* and *L. noctivagans* in southeastern Alaska has not been established because few data are available for these species (Chapters 2 and 3). Foraging strategies, prey availability, and reproductive success of these species should be assessed in southeastern Alaska.

Although questions remain about how habitat modification in southeastern Alaska affects bat populations, this study suggests that present levels of timber harvest will have a detrimental effect on these bat populations. I provide evidence that neither clearcuts, nor second-growth forests provide habitat used by most southeastern Alaska bats during the summer. I also provide evidence that unharvested old-growth forests and riparian zones provide habitats that are used frequently by bats.

Chapter Five

Summary

I have refined the range and distribution limits of the five bat species in Alaska, and further conclude that *Eptesicus fuscus* is not a regular member of Alaska's fauna. *Myotis lucifugus, M. californicus, M. keenii, M. volans* occur in southeastern Alaska year-round. *Lasionycteris noctivagans* may migrate to southeastern Alaska in winter. *Myotis lucifugus* is the most commonly encountered bat species in southeastern Alaska and throughout the state.

Data provided in chapter two are a starting point for future studies on bat species distribution and latitudinal limits in Alaska. Further investigation should clarify patterns of distribution, abundance, and reproduction throughout Alaska. Little is known about the environmental factors that influence bat distribution in Alaska. However, the factors I have discussed furnish a basis for further study. With knowledge of current species distribution and range limits, climatic regimes, and genetic relationships, it may be possible to document the impact of global climatic change in the future by documenting shifts in bat species distribution and latitudinal limits.

The habitat requirements of *M. keenii* and the potential effects of forest modification on this species remain unclear because of its uncertain ecology and apparent rarity. What is certain is that significant habitat modification has occurred in southeastern Alaska in the past 50 years (United States Department of Agriculture 1991; 1993). Federal law in the United States requires public land managers to inventory and maintain viable populations of wildlife affected by land management practices, such as timber harvest (United States Congress 1970; 1976). Therefore, the

status and ecology of *M. keenii* need further documentation. Continuing habitat modification may negatively impact the viability of this species in southeastern Alaska.

This study supports the concept that old-growth forests and riparian areas provide important roosting and foraging habitat for the five bat species in southeastern Alaska. Extensive past and future harvest in southeastern Alaska (United States Department of Agriculture 1991; 1993; *in press*) suggests a significant impact on these species. My data also indicate that clearcuts show little bat activity, perhaps because clearcuts do not provide roosting structure. Closed-canopy second-growth is not used by bats in southeastern Alaska. Old-growth characteristics that provide suitable roost sites for bats do not develop until at least 150 years after harvest. Large tracts of such second-growth forests may impact bat species viability in the naturally fragmented forests of southeastern Alaska's Alexander Archipelago. Therefore, planning and environmental assessment processes for public lands in the region should include this information when considering the effects of land management practices. In addition, further species inventory and ecological studies are needed to fully assess the impacts of land management practices on the bats in southeastern Alaska.

Southeastern Alaska is unique among high-latitude archipelagos because of its large number and high diversity of caves (Aley et al. 1993; Baichtal 1995). Personal observations suggest that bats occupy caves during cold spells in the winter, but leave these caves during warmer spells. Documentation of winter activity patterns and foraging strategies in relation to weather patterns and habitat type will be important in determining the effects of timber harvest on bats.

My study provides evidence that the ecology of *M. lucifugus* in southeastern Alaska's Alexander Archipelago differs somewhat from conspecifics at lower latitudes. Reproduction and diet appear to differ between *M. lucifugus* in southeastern Alaska and conspecifics in similar rainforests at lower latitudes. Ecology of *M. volans, M. keenii, M. californicus* and *L. noctivagans* in southeastern Alaska has not been established

because no data are available for these species. Foraging strategies, prey availability, and reproductive success of these species in southeastern Alaska should be assessed.

Although questions remain about how habitat modification in southeastern Alaska affects bat populations, this study suggests that present levels of timber harvest will have a detrimental effect on these bat populations. I provide evidence that neither clearcuts nor second-growth forests provide habitat utilized by most southeastern Alaska bats during the summer. I also provide evidence that unharvested old-growth forests and riparian zones provide habitat that is used consistently by these bats in summer.

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APPENDIX I

List of Museum Specimens and Locality

Myotis lucifugus (Le Conte, 1831)

Central (20 specimens). Minto Lks., 65° 00' N 148° 30' W (4 UAM); Smallwood Cr., 64° 55' N 147° 15' W (1 UAM); 18 mi Old Nenana Hwy, 64° 51' N 148° 15' W (1 UAM); College, 64° 50' N 147° 50' W (2 UAM, 1 UMDZ); Fairbanks, 64° 50' N 147° 30' W (1 UAM); North Pole, 64° 45' N 147° 21' W (4 UAM); 5 mi S of North Pole, 64° N 147° W (1 UAM); Harding Lk., 64° 45' N 146° 50' W (2 MVZ); S of Bonanza Cr. experimental forest, 64° 42' N 148° 16' W (1 UAM); Sleetmute, 61° 42' N 157° 10' W (1 CM); Birch Lk. at mi 65 Richardson Hwy, 64° 20' N 146° 20' W (1 UAM).

Southwestern (51 specimens). Mainland: Pedro Bay, 59° 42' N 154° 13' W (1 CM); Lk Iliamna, 59° 30' N 154° 4' W (1 USNM); King Salmon, 58° 41' N 156° 39' W (1 UAM). Afognak Is.: Kitoi Bay, 58° 11' N 152° 21' W (1 CM). Kodiak Is.: 57° 20' N 153° 22' W (9 USNM, 1 MCZ); Chiniak, 57° 37' N 157° 7' W (18 UAM); Uyak Bay at Larsen Bay, 47° 32' N 153° 58' W (5 FMNH, 14 KU).

Southcentral (23 specimens). Palmer, 61° 36' N 149° 6' W (2 CM); Chitistone R., 61° 26' N 142° 31' W (1 UAM); Anchorage, 61° 13' N 149° 53' W (1 USNM, 1 FMNH, 1 UIMNH); Peters Cr., 61° 24' N 149° 26' W (1 KU); Port Nellie Juan, 60° 33' N 148° 9' W (1 MVZ); Hope, 60° 55' N 149° 38' W (2 CM); Cordova

gun club, 60° 30' N 145° 25' W (10 UAM); 6 mi S. of Wasilla, 61° N 149° W (3 UIMNH).

Southeastern (185 specimens). Mainland: Bartlett Cove, 58° 27' N 135° 53' W (10 UAM); Situk R., 59° 26' N 139° 33' W (2 ROM); Juneau near Salmon Cr., 58° 37' N 134° 27' W (1 UAM); Andrew Cr., N of Mt. Rynda, 56° 40' N 132° 13' W (5 UAM); Bailey Bay Hot Spr., 55° 58' N 131° 37' W (1 UAM); Boca de Quadra Fjord, head of Marten Arm, 55° 10' N 130° 31' W (3 MVZ); Salmon R. at Fish Cr., 55° 58' N 130° 2' W (5 UAM); Hyder, 55° 55' N 130° 1' W (40 UAM); Mouth of Chickamin R. at Wolf Cabins, 55° 49' N 130° 54' W (3 UAM); Hugh Smith Lk, 55° 6' N 130° 40' W (3 UAM). Chichagof Is.: Hoonah, 58° 06' N 135° 26' W (20 UAM); White Sulfur Spr., 57° 6' N 134° 20' W (4 UAM); Kadashan R., 57° 42' N 135° 13' W (1 UAM). Admiralty Is.: Windfall Harbor 57° 50' N 134° 18' W (4 UAM); Mole Harbor, 57° 40' N 134° 3' W (1 MVZ). Baranof Is.: Sitka, 57° 3' N 135° 20' W (6 USNM, 1 MCZ, 2 CM); Red Bluff Bay, 56° 50' N 134° 42' W (8 MVZ, 2 KU). Mitkof Is.: Petersburg Reservoir, 56° 55' N 133° 47' W (1 UAM); Petersburg, 56° 48' N 132° 58' W (6 UAM). Wrangell Is.: Pond near Fool's Inlet rd., 56° 17' N 132° 5' W (1 UAM). Prince of Wales Is.: 55° 30' N 132° 30' W (24 UAM). Revillagigedo Is.: Portage Cove, 55° 46' N 131° 2' W (14 MVZ); Loring, 55° 36' N 131° 39' W (4 UAM, 4 USNM); Ward Lk, 55° 24' N 131° 42' W (3 UAM); Ketchikan, 55° 20' N 131° 38' W (3 USNM); Herring Bay, 55° 20' N 131° 31' W (1 UAM). Grant Is.: 55° 33' N 131° 43' W (1 LACM). Dall Is.: Essowah Lks, 54° 47' N 132° 52' W (1 UAM).

Myotis volans (H. Allen, 1866)

Southeastern (5 specimens). Admiralty Is.: Mole Harbor, 57° 40' N 134° 3' W (1 MVZ). Wrangell Is.: Mt. Dewey trail head, 56° 28' N 132° 23' W (2 UAM, 1 ADFG). Prince of Wales Is.: Polk Inlet 55° 20' N 132° 30' W (1 UAM).

Myotis keenii (Merriam, 1895)

Southeastern (3 specimens). Chichagof Is.: Hoonah, 58° 06' N 135° 26' W (1 UAM). Wrangell Is.: Wrangell, 56° 28' N 132° 22' W (1 USNM). Prince of Wales Is.: Turn Cr., 56° 10' N 133° 18' W (1 UAM).

Myotis californicus (Audubon and Bachman, 1842)

Southeastern (5 specimens). Prince of Wales Is.: El Capitan cave, 56° 10' N 133° 19' W (3 UAM). Long Is.: Howkan, 54° 52' N 132° 48' W (2 MVZ).

Lasionycteris noctivagans (Le Conte, 1831)

Southeastern (4 specimens). Mainland: Taku River, Canyon Is., 58° 43' N 133° 40' W (1, AMNH). Wrangell Is.: 15 km S of Wrangell, 56° 22' N 132° 22' W (1 UAM). Mitkof Is.: Petersburg, 56° 45' N 132° 56' W (1 UAM). Revillagigedo Is.: 4 mi N Tongass Hwy, Ketchikan, 55° 20' N 131° 38' W (1 UAM).

Eptesicus fuscus (Palisot de Beauvois, 1796)

Central (1 specimen). Shaw Creek, 64° 29' N 145° 5' W (1 UMDZ).

APPENDIX II

List of Museums Contacted

Museum acronyms follow Yates et al. (1987).

Museums That Hold Alaska Bat Specimens:

Alaska Department of Fish and Game Collection, Anchorage Alaska (ADFG)

American Museum of Natural History (AMNH)

Carnegie Museum of Natural History (CM)

Field Museum of Natural History (FMNH)

University of Kansas Museum of Natural History (KU)

Los Angeles County Museum (LACM)

Museum of Comparative Zoology, Harvard University (MCZ)

Museum of Vertebrate Zoology, University of California, Berkeley (MVZ)

Royal Ontario Museum (ROM)

University of Alaska Museum (UAM)

University of Illinois Museum of Natural History (UIMNH)

University of Michigan Museum of Zoology (UMDZ)

U. S. National Museum of Natural History (USNM)

Museums That Do Not Hold Alaska Bat Specimens:

University of Alberta Museum of Zoology, Alberta

British Columbia Provincial Museum, Victoria

Canadian Museum of Nature, Ottawa

California Academy of Science

San Diego Natural History Museum

Santa Barbara Museum of Natural History

UCLA Bird and Mammal Collection

Louisiana State University Museum of Zoology

Michigan State University Museum

Texas A and M University, Texas Cooperative Wildlife Collection

University of Washington Burke Washington State Museum

Washington State University, Charles R. Conner Museum